# Some color in the desert: description of a new species of Liolaemus (Iguania: Liolaemidae) from southern Peru, and its conservation status 

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#### Abstract

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#### Abstract

The desert of southern Peru and northern Chile is an area with a high degree of endemism in squamate reptiles. In this work, an endemic new species is described in the genus Liolaemus with a restricted geographical distribution on the western slopes of the La Caldera batholith in the Department of Arequipa, southern Peru, that inhabits the Desert province of southern Peru, between 1,800 and 2,756 m asl. The new species is characterized by a unique combination of morphological and molecular characters that distinguish it from all other Liolaemus species, and it is included in the L. reichei clade within the $L$. montanus group. Evidence presented shows that the category of threat corresponds to Endangered under the IUCN Red List criteria.


Keywords. Arequipa, coastal desert, Endangered, La Caldera batholith, Liolaemus insolitus, lizard, Reptilia
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## Introduction

The Desert province of the South American Transition Zone (sensu Morrone 2014), a biogeographic area that corresponds to a narrow strip along the Pacific Ocean coast from northern Peru to northern Chile (Fig. 1), is located in southern Peru near the Chilean border. This desert contains one of the most hyper-arid deserts in the world, the La Joya desert, which includes areas with zero annual rainfall (Valdivia-Silva et al. 2012) and soils with characteristics like the surface of Mars (Valdivia-Silva et al. 2011). The southern portion of the Desert province harbors a distinctive biota characterized by many endemic plants and animals (e.g., Gutiérrez et al. 2019; Málaga et
al. 2020). The knowledge of the amphibians and reptiles in this area remains scarce compared to the desert areas in Chile and Argentina (Escomel 1929; Dixon and Wright 1975; Péfaur et al. 1978a,b; Cei and Péfaur 1982; Frost 1992; Carrillo and Icochea 1995; Zeballos et al. 2002; Gutiérrez et al. 2010; Abdala y Quinteros 2014); although in recent years three species of Liolaemus lizards were described from this region (Aguilar-Puntriano et al. 2019; Villegas-Paredes et al. 2020).

The South American genus Liolaemus comprises more than 270 formally described species (Abdala and Quinteros 2014; Gutiérrez et al. 2018; Abdala et al. 2019; Villegas-Paredes et al. 2020; Chaparro et al. 2020). These lizards occupy habitats ranging from hot areas, such as


Fig. 1. Biogeographic regionalization proposed by Morrone (2014), showing the limits of the Desert province and Atacama province. The geoform La Caldera batholith, adapted from Ramos (2008), is also shown.
the Atlantic coast of southern Brazil and the continental deserts in Chile, Peru, and Argentina, to very cold regions such as Patagonia in Argentina or the high Central Andes in Peru and Bolivia, and reaching elevations greater than $5,000 \mathrm{~m}$ asl (Abdala and Quinteros 2014; Gutiérrez et al. 2018; Abdala et al. 2020; Ruiz et al. 2019; Quinteros et al. 2020).

The great diversity within Liolaemus includes a few species with a wide distribution range, such as $L$. darwinii (Abdala 2007), L. multicolor (Abdala et al. 2020), and $L$. wiegmannii (Villamil et al. 2019), in addition to a large number of species with very restricted distributions, e.g., L. halonastes (Lobo et al. 2010), L. rabinoi (Abdala et al. 2017), and L. balagueri (Villegas-Paredes et al. 2020). Liolaemus is divided into the subgenera Eulaemus and Liolaemus sensu stricto (Laurent 1983, 1985; Schulte et al. 2001). Within these subgenera, a large number of monophyletic groups have been named (Etheridge 1995; Lobo 2005; Avila et al. 2006; Abdala 2007; Quinteros 2013; Breitman et al. 2011; Abdala et al. 2020).

One of the large groups within Eulaemus is the L. montanus group (Etheridge 1995; Abdala et al. 2020), which is made up of more than 60 described species, and several unnamed species (Abdala et al. 2020). In general, the $L$. montanus group has been studied in recent years from various branches of biology (Halloy et al. 2013;

Troncoso-Yañez 2013; Riveros-Riffo and Torres-Murua 2015; Ruiz de Gamboa and Ortiz-Zapara 2016; AguilarKirigin and Abdala 2016; Aguilar-Kirigin et al. 2016; Quipildor et al. 2018), however the taxonomy (Abdala et al. 2008, 2009, 2013; Lobo et al. 2010; Quinteros and Abdala 2011; Gutiérrez et al. 2018; Ruiz de Gamboa et al. 2018; Aguilar et al. 2017; Aguilar-Puntriano et al. 2019; Abdala et al. 2019), and the phylogenetic hypotheses (Aguilar et al. 2017; Abdala et al. 2020; Chaparro et al. 2020), are the areas that have been most developed, providing essential information for understanding the distribution and diversity of the group. However, essential knowledge gaps remain, including sensitive and important issues such as conservation and natural history. In total, 17 species of $L$. montanus group have been reported for Peru (Chaparro et al. 2020), with six species recorded in the last three years (Gutiérrez et al. 2018; Aguilar-Puntriano et al. 2019; Chaparro et al. 2020; Villegas-Paredes et al. 2020). Additionally, in recent integrative taxonomy studies (Aguilar et al. 2017; Abdala et al. 2020), several populations of unnamed species representing independent lineages have been proposed.

While the $L$. montanus species group largely inhabits cold and high-altitude environments, the species of the $L$. reichei clade (sensu Abdala et al. 2020) occupy coastal habitats of northern Chile and southern Peru (e.g., Aguilar-

Table 1. Species list of Liolaemus reichei clade.

| Species name | Author(s) | Distribution |
| :--- | :---: | :---: |
| Liolaemus audituvelatus | (Núñez and Yáñez 1983) | Chile: Antofagasta/ Atacama Regions |
| Liolaemus balagueri | Villegas et al. 2020 | Peru: Arequipa Department |
| Liolaemus chiribaya | Aguilar et al. 2019 | Peru: Moquegua Department |
| Liolaemus insolitus | Cei y Péfaur 1982 | Peru: Arequipa Department |
| Liolaemus nazca | Aguilar et al. 2019 | Peru: Arequipa Department |
| Liolaemus poconchilensis | Valladares 2004 | Peru: Tacna Department, Chile: Arica Region |
| Liolaemus reichei | (Werner 1907) | Chile: Tarapaca Region |
| Liolaemus stolzmanni | (Steindachner 1891) | Chile: Antofagasta Region |
| Liolaemus torresi | (Nuñez et al. 1891) | Chile: Antofagasta Region |

Puntriano et al. 2018; Villegas-Paredes et al. 2020). The known diversity of the $L$. reichei clade (Table 1) has increased considerably in recent years with the description of $L$. balagueri (Villegas-Paredes et al. 2020), as well as L. chiribaya and L. nazca (Aguilar-Puntriano et al. 2019). Various taxonomic and phylogenetic hypotheses have been proposed recently for the L. reichei group (Langstroth 2011; Aguilar-Puntriano et al. 2018; Ruiz de Gamboa et al. 2018; Valladares et al. 2018; Abdala et al. 2020; VillegasParedes et al. 2020; Chaparro et al. 2020). Abdala et al. (2020) recovered seven candidate species within their $L$. reichei clade which are all very close phylogenetically to L. insolitus, a species with a distribution restricted to its type locality in the coastal desert of the Department of Arequipa. In the present study, the taxonomic hypothesis of one of these unnamed populations is evaluated using the general or unified concept of species (De Queiroz 1998, 2007). This concept defines a species as an entity that represents independent historical lineages or divergent lineages of metapopulations. Our criteria to determine the independence of this lineage is based on Total Evidence, such as phylogenetics (molecular and morphological), multivariate statistical analysis, and the description of unique morphological characters; and the results provide decisive evidence to describe it as a new species of Liolaemus.

## Materials and Methods

Images and maps. Photographs of live specimens were taken using a digital camera Canon sx50 hs. Closeup photographs of the holotype (preserved) were taken with a digital camera Canon EOS Rebel T5. Maps were elaborated using ArcMap 10.3, and use coordinates previously cited by Aguilar et al. (2016), Gutiérrez et al. (2018), and Chaparro et al. (2020). Type localities were taken from the original manuscripts of the species descriptions. Coordinates of the records reported here were obtained with a GPS device (datum WGS84), Garmin Etrex 30. The regionalization map was elaborated using shape files design from Löwenberg-Neto, which follows Morrone (2014).

Material examined. Specimens of Liolaemus examined were from the Museo de Historia Natural de la Universidad Nacional de San Agustín de Arequipa, Perú (MUSA); Museo de Biodiversidad del Perú, Cusco, Perú (MUBI); Fundación Miguel Lillo, Tucumán, Argentina (FML); and Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM). Collected specimens of Liolaemus were captured by hand within the locality of La Caldera batholith, District of Uchumayo, Province of Arequipa, Department of Arequipa, Peru. Specimens were euthanized with a $1 \%$ Halatal solution, fixed with $10 \%$ formaldehyde, and stored in $70 \%$ alcohol. Prior to fixation, a sample of muscle was collected for DNA extraction and fixed in $96 \%$ ethanol. Collected specimens are deposited in the collections of MUSA and MUBI. Appendix I details the specimens used for the first time here, as well as those reanalyzed for the present work but previously examined in Abdala and Quinteros (2008), Abdala et al. (2008, 2009, 2013), Quinteros et al. (2008), Quinteros and Abdala (2011), Gutiérrez et al. (2018), and Abdala et al. (2020). Additional data were obtained from the literature for $L$. erroneous (Núñez and Yáñez 1984), L. omorfi (Demangel et al. 2015), and L. stolzmanni (Langstroth 2011).

Conservation status and endemism. The IUCN (2001, 2020) criteria were used to categorize the new species. The extent of occurrence (EOO), and area of occupancy (AOO), were obtained using the GeoCat tool (http:// geocat.kew.org/), which is a tool that follows IUCN criteria. The endemic concept and restricted range of distribution followed Bruchmann and Hobohm (2014), IUCN (2016), Kier and Barthlott (2001), and NogueraUrbano (2017).

Morphological data. Morphological characters utilized in taxonomic studies of Liolaemus were studied here, mainly those described or cited by Laurent (1985), Etheridge (1995, 2000), Abdala (2007), Abdala and Juárez (2013), Gutiérrez et al. (2018), Aguilar-Puntriano et al. (2018), Villegas-Paredes et al. (2020), and Abdala et al. (2020). The coloration description was based on live specimens and digital photographs taken in the field. Color
pattern terminology follows Lobo and Espinoza (1999), Abdala (2007), and Abdala et al. (2020). Examination of scalation or pholidosis was performed using a binocular stereoscope ( $10-40 \mathrm{x}$ ), and morphometric measurements were made with a Mitutoyo caliper with precision of 0.01 mm . The morphometric variables were measured three times on the same individual, and the mean value for each species was used in the statistical analyses. Only adult males were used in the multivariate analysis to avoid confounding effects of intraspecific allometric variation, and to avoid confusion in the multivariate analyses due to possible sexual dimorphism (Losos 1990; Abdala et al. 2019). All bilateral characters were measured on the right side. The measured morphometric traits and meristic characters counted follow Abdala et al. (2019) [Appendix II].

DNA extraction, amplification, and sequencing. Total genomic DNA was extracted from samples of muscle using the GenElute mammalian genomic DNA miniprep kit (Sigma-Aldrich), according to the manufacture's instructions. A fragment of approximately 1,174 base pairs of the mitochondrial gene cytochrome b (cyt- $b$ ) was amplified by polymerase chain reaction (PCR), using the primers IguaCytob_ F2 (5'-CCACCGTTGTTATTCAACTAC-3') and IguaCytob_R2 (5'-GGTTTACAAGACCAATGCTTT-3') [Corl et al. 2010]. Each reaction contained 1x PCR buffer ( KCl ), $2.5 \mathrm{mM} \mathrm{MgCl} 2,0.25 \mathrm{mM}$ each dNTP, $0.1 \mu \mathrm{M}$ each primer, 1 unit of Taq DNA polymerase (Thermo Scientific), and $1 \mu \mathrm{~L}$ DNA extract. PCR cycling consisted of a 5 min initial denaturation at $94^{\circ} \mathrm{C}, 35$ cycles of 30 sec at $94{ }^{\circ} \mathrm{C} ; 30 \mathrm{sec}$ at $55^{\circ} \mathrm{C} ; 60 \mathrm{sec}$ at $72^{\circ} \mathrm{C}$, and a final elongation step of 2 min at $72^{\circ} \mathrm{C}$. The PCR product was visualized on $1.5 \%$ agarose gel stained with Gel-Red (Biotium, Inc.), and subsequently sent to Macrogen, Inc. (Seoul, Republic of Korea) for purification and direct sequencing. The nucleotide sequence was visualized and edited using 4 Peaks software (http://nucleobytes. com/4peaks/) and checked manually, and nucleotides with ambiguous positions were clarified. The sequences newly obtained in this study are publically available in GenBank (see Table 2).

Statistical analysis. A Principal Component Analysis (PCA) was employed to analyze morphological variation, and discriminant function analyses (DFA) were used to verify morphological variation between and within each Liolaemus species employing a jackknife classification matrix (Manly 2000; McCune and Grace 2002; Quinn and Keough 2002; Zar 2010). Based on the existing phylogenetic results (Abdala et al. 2020) and those obtained, four species of $L$. reichei clade distributed in Peru (L. balagueri, L. chiribaya, L. insolitus, and $L$. $n a z c a$ ), and the new species proposed here were used as comparative groups for building the PCA and the DFA. Normal distributions of the morphometric data were
examined using the Kolmogorov-Smirnov test ( $P<0.05$ ), and homoscedasticity was evaluated with Levene's test. To reduce the effect of non-normal distributions of the morphological data, all continuous variables were $\log _{10}$ transformed and meristic variables were square root transformed (Irschick and Losos 1996; Sokal and Rohlf 1998; Peres-Neto and Jackson 2001).

All operational taxonomic units were analyzed by two distinct treatments. The PCA analysis was performed to evaluate the distribution of individuals corresponding to the five species (L. balagueri, L. chiribaya, L. insolitus, $L$. nazca, and Liolaemus sp. nov.) in the multivariate space. The PCA was based on the correlation matrices of the morphological variables to reduce dimensionality of the data (Quinn and Keough 2002; Lovett et al. 2000). The PCA and DFA were evaluated separately for continuous and meristic characters, following the recommendations of certain authors not to join both matrices in the multivariate analyses, although there is no mathematical consensus on this approach (McGarigal et al. 2000). The PCA evaluates relationships within a single group of interdependent variables regardless of any relationships that they may have outside of that group of variables. After the PCA was performed, and the lineal combinations that explained the highest variation were extracted, DFA was performed independently for continuous and meristic morphological characters, to identify the combination of morphological characters that best differ between the groups identified by the PCA. The DFA produces a linear combination of variables that maximizes the probability of correctly assigning observations to predetermined groups, and simultaneously, new observations can be classified into one of the groups, providing likelihood values of such classification (McGarigal et al. 2000; Van den Brink et al. 2003). All statistical analyses were performed using Statistica software, version 7.0 (http://www.statsoft.com).

Phylogenetic analysis. Three matrices were constructed, including: (1) morphological data; (2) molecular characters (cyt-b); and (3) both morphological and molecular data. Total Evidence and morphological phylogenetic analysis were performed using the matrix of Abdala et al. (2020). The morphological matrix includes 306 characters and 105 terminals (with Ctenoblepharys adspersa and Phymaturus palluma as an "outgroup" and 96 terminals of L. montanus group). The Total Evidence matrix included 105 terminals and 3,390 characters. Parsimony was used as the optimality criterion, only selecting the shortest trees or those with the fewest homoplasies. TNT version 1.5 (Tree Analysis Using New Technology; Goloboff et al. 2003) was employed to generate the phylogenetic hypotheses. Continuous characters were analyzed following Goloboff et al. (2006), and were standardized using the function mkstandb.run. For this analysis, the value of two was considered as the highest transformation cost. Heuristic searching was used to find the shortest trees or those with the smallest number of steps. The matrix was analyzed

Table 2. GenBank codes and voucher information of Liolaemus and outgroup specimens sequenced for this study.

| Species names | Voucher code | cyt-b | Source |
| :---: | :---: | :---: | :---: |
| Ctenoblepharys adspersa (outgroup) | BYU 50502 | MH981364 | Aguilar-Puntriano et al. 2018 |
| L. annectens | BYU 50489 | KX826616 | Aguilar et al. 2016 |
| L. annectens | BYU 50486 | KX826615 | Aguilar et al. 2016 |
| L. annectens | BYU 50491 | KX826617 | Aguilar et al. 2016 |
| L. annectens "Lampa" | MUSM 31433 | KX826618 | Aguilar et al. 2016 |
| L. balagueri | MUSA 5575 | MK568539 | Villegas-Paredes et al. 2020 |
| L. balagueri | MUSA 5576 | MK568538 | Villegas-Paredes et al. 2020 |
| L. chiribaya | BYU 51568 | MH981365 | Aguilar-Puntriano et al. 2018 |
| L. etheridgei | BYU 50494 | KX826620 | Aguilar et al. 2016 |
| L. etheridgei | BYU 50495 | KX826621 | Aguilar et al. 2016 |
| L. etheridgei | BYU 50497 | KX826622 | Aguilar et al. 2016 |
| L. etheridgei | BYU 50493 | KX826619 | Aguilar et al. 2016 |
| L. etheridgei | BYU 50499 | KX826623 | Aguilar et al. 2016 |
| L. etheridgei | MUSM 31494 | KX826625 | Aguilar et al. 2016 |
| L. stolzmanni | LNC 138 | MH184793 | Ruiz De Gamboa et al. 2018 |
| L. stolzmanni | MR 213 | MH184794 | Ruiz De Gamboa et al. 2018 |
| L. torresi | LNC 146 | MH184797 | Ruiz De Gamboa et al. 2018 |
| L. torresi | LNC 134 | MH184795 | Ruiz De Gamboa et al. 2018 |
| L. torresi | LNC 133 | MH184796 | Ruiz De Gamboa et al. 2018 |
| L. insolitus | MUSM 31490 | KX826627 | Aguilar et al. 2016 |
| L. insolitus | BYU 50462 | KX826626 | Aguilar et al. 2016 |
| L. dorbignyi | LJAMMCNP 5002 | KF968848 | Olave et al. 2014 |
| L. eleodori | LJAMMCNP 2709 | KF968850 | Olave et al. 2014 |
| L. audituvelatus | LNC 136 | MH184785 | Ruiz De Gamboa et al. 2018 |
| L. audituvelatus | LNC 86 | MH184779 | Ruiz De Gamboa et al. 2018 |
| L. audituvelatus | ER1 | MH184780 | Ruiz De Gamboa et al. 2018 |
| L. audituvelatus | MUAP104 | MH184782 | Ruiz De Gamboa et al. 2018 |
| L. audituvelatus | SSUC-Re760 | MH184783 | Ruiz De Gamboa et al. 2018 |
| L. audituvelatus | LNC 135 | MH184784 | Ruiz De Gamboa et al. 2018 |
| L.vallecurensis | LJAMMCNP 650 | KF968960 | Olave et al. 2014 |
| L. nazca (L. "Nazca") | BYU 50472 | KX826673 | Aguilar et al. 2016 |
| L. nazca (L. "Nazca") | BYU 50507 | KX826674 | Aguilar et al. 2016 |
| L. nazca (L. "Nazca") | BYU 50508 | KX826675 | Aguilar et al. 2016 |
| L. nazca (L. "Nazca") | MUSM 31523 | KX826676 | Aguilar et al. 2016 |
| L. nazca (L. "Nazca") | MUSM 31524 | KX826677 | Aguilar et al. 2016 |
| L. ortizi | MUSM 31513 | KX826633 | Aguilar et al. 2016 |
| L. ortizi | MUSM 31514 | KX826634 | Aguilar et al. 2016 |
| L. aff. poconchilensis | MUSM 31545 | KX826637 | Aguilar et al. 2016 |
| L. poconchilensis | MUSM 31543 | KX826635 | Aguilar et al. 2016 |
| L. poconchilensis | MUSM 31544 | KX826636 | Aguilar et al. 2016 |
| L. poconchilensis | MZUC43498 | MH184798 | Ruiz De Gamboa et al. 2018 |
| L. poconchilensis | MZUC43497 | MH184799 | Ruiz De Gamboa et al. 2018 |

Table 2 (continued). GenBank codes and voucher information of Liolaemus and outgroup specimens sequenced for this study.

| Species names | Voucher code | cyt-b | Source |
| :---: | :---: | :---: | :---: |
| L. polystictus | MUSM 31451 | KX826642 | Aguilar et al. 2016 |
| L. polystictus | MUSM 31446 | KX826641 | Aguilar et al. 2016 |
| L. qalaywa | MUBI 12081 | MT366061 | Chaparro et al. 2020 |
| L. qalaywa | MUBI 12099 | MT366062 | Chaparro et al. 2020 |
| L. "Apurimac" | MUSM 27694 | MH981371 | Aguilar-Puntriano et al. 2018 |
| L. robustus | MUSM 31504 | KX826646 | Aguilar et al. 2016 |
| L. robustus | MUSM 31508 | KX826648 | Aguilar et al. 2016 |
| L. robustus | MUSM 31505 | KX826647 | Aguilar et al. 2016 |
| L. robustus | BYU 50483 | KX826643 | Aguilar et al. 2016 |
| L. thomasi | BYU 50469 | KX826680 | Aguilar et al. 2016 |
| L. thomasi | BYU 50466 | KX826678 | Aguilar et al. 2016 |
| L. thomasi | MUSM 31516 | KX826681 | Aguilar et al. 2016 |
| L. thomasi | BYU 50467 | KX826679 | Aguilar et al. 2016 |
| L. thomasi | MUBI 5925 | MT366060 | Chaparro et al. 2020 |
| L. signifer | MUSM 31443 | KX826656 | Aguilar et al. 2016 |
| L. signifer | MUSM 31434 | KX826654 | Aguilar et al. 2016 |
| L. signifer | BYU 50444 | KX826652 | Aguilar et al. 2016 |
| L. signifer | BYU 50357 | KX826651 | Aguilar et al. 2016 |
| L. signifer | BYU 50350 | KX826649 | Aguilar et al. 2016 |
| L. signifer | MUSM 31437 | KX826655 | Aguilar et al. 2016 |
| L. signifer | BYU 50355 | KX826650 | Aguilar et al. 2016 |
| L. signifer | MUSM 31447 | KX826657 | Aguilar et al. 2016 |
| L. signifer | MUSM 29110 | KX826653 | Aguilar et al. 2016 |
| L. melanogaster | BYU 50151 | KX826628 | Aguilar et al. 2016 |
| L. melanogaster | MUSM 31472 | KX826630 | Aguilar et al. 2016 |
| L. melanogaster | MUSM 31475 | KX826631 | Aguilar et al. 2016 |
| L. melanogaster | BYU 50154 | KX826629 | Aguilar et al. 2016 |
| L. victormoralesii (L. "AbraToccto") | MUSM 31371 | KX826665 | Aguilar et al. 2016 |
| L. victormoralesii (L. "AbraToccto") | MUSM 31374 | KX826667 | Aguilar et al. 2016 |
| L. victormoralesii (L. "AbraToccto") | MUSM 31373 | KX826666 | Aguilar et al. 2016 |
| L. victormoralesii (L. "AbraToccto") | BYU 50426 | KX826661 | Aguilar et al. 2016 |
| L. victormoralesii (L. "AbraToccto") | MUSM 31461 | KX826668 | Aguilar et al. 2016 |
| L. victormoralesii (L. "AbraToccto") | BYU 50430 | KX826663 | Aguilar et al. 2016 |
| L. victormoralesii (L. "AbraToccto") | MUSM 31462 | KX826669 | Aguilar et al. 2016 |
| L. victormoralesii (L. "AbraToccto") | BYU 50431 | KX826664 | Aguilar et al. 2016 |
| L. victormoralesii (L. "AbraToccto") | BYU 50428 | KX826662 | Aguilar et al. 2016 |
| L. victormoralesii (L. "AbraToccto") | MUSM 31464 | KX826670 | Aguilar et al. 2016 |
| L. victormoralesii (L. "AbraToccto") | MUSM 31465 | KX826671 | Aguilar et al. 2016 |
| L. victormoralesii (L. "AbraToccto") | MUSM 31468 | KX826672 | Aguilar et al. 2016 |
| L. williamsi | BYU 50463 | KX826684 | Aguilar et al. 2016 |
| L. williamsi | MUSM 31485 | KX826687 | Aguilar et al. 2016 |
| L. williamsi | BYU 50143 | KX826682 | Aguilar et al. 2016 |

Table 2 (continued). GenBank codes and voucher information of Liolaemus and outgroup specimens sequenced for this study.

| Species names | Voucher code | cyt-b | Source |
| :---: | :---: | :---: | :---: |
| L. williamsi | BYU 50464 | KX826685 | Aguilar et al. 2016 |
| L. williamsi | BYU 50144 | KX826683 | Aguilar et al. 2016 |
| L. williamsi | MUSM 31486 | KX826688 | Aguilar et al. 2016 |
| L. williamsi | BYU 50465 | KX826686 | Aguilar et al. 2016 |
| L. "AbraApacheta" | MUSM 31481 | KX826660 | Aguilar et al. 2016 |
| L. "AbraApacheta" | BYU 50145 | KX826658 | Aguilar et al. 2016 |
| L. "AbraApacheta" | BYU 50148 | KX826659 | Aguilar et al. 2016 |
| L. polystictus "Castrovirreyna" | MUSM 31454 | KX826639 | Aguilar et al. 2016 |
| L. polystictus "Castrovirreyna" | BYU 50630 | KX826638 | Aguilar et al. 2016 |
| L. polystictus "Castrovirreyna" | BYU 31455 | KX826640 | Aguilar et al. 2016 |
| L. robustus "MinaMartha" | BYU 50438 | KX826644 | Aguilar et al. 2016 |
| L. robustus "MinaMartha" | MUSM 31439 | KX826645 | Aguilar et al. 2016 |
| L. annectens | LDHV 73 | MT773391 | This study |
| L. aff. annectens | LECG 078 | MT773392 | This study |
| L. "Cotahuasi" | RGP 6031 | MT773393 | This study |
| L. "Cotahuasi" | MDUM 006 | MT773394 | This study |
| L. "Cotahuasi" | MDUM 005 | MT773395 | This study |
| L. "Cotahuasi" | MDUM 004 | MT773396 | This study |
| L. aff. qalaywa 1 | MDUM 001 | MT773397 | This study |
| L. aff. qalaywa 1 | MDUM 002 | MT773398 | This study |
| L. aff. qalaywa | MDUM 017 | MT773399 | This study |
| L. aff. qalaywa | MDUM 014 | MT773400 | This study |
| L. aff. qalaywa | MDUM 007 | MT773401 | This study |
| L. aff. qalaywa | VOI 009 | MT773402 | This study |
| L. aff. qalaywa | VOI 006 | MT773403 | This study |
| L. chiribaya | AQR 003 | MT773404 | This study |
| L. chiribaya | AQR 004 | MT773405 | This study |
| L. aff. insolitus 4 | RGP 6249 | MT773406 | This study |
| L. sp. nov. (described herein) | MUSA 1766 | MT773407 | This study |
| L. sp. nov. (described herein) | MUBI 13522 | MT773408 | This study |
| L. sp. nov. (described herein) | MUBI 14417 | MT773409 | This study |
| L. aff. insolitus6 | MUSA 1769 | MT773410 | This study |
| L. aff. insolitus6 | MUSA 1770 | MT773411 | This study |
| L. aff. insolitus6 | MUSA 1771 | MT773412 | This study |
| L. insolitus | AQR 001 | MT773413 | This study |
| L. insolitus | AQR 002 | MT773414 | This study |
| L. aff balagueri | LDHV 005 | MT771288 | This study |
| L. aff. insolitus 2 | RGP 6147 | MT773415 | This study |
| L. aff. insolitus8 | RGP 6154 | MT773416 | This study |

using the "implied weights" method (Goloboff 1993). The value of the constants $\mathrm{K}=14$ (morphological analysis) and $\mathrm{K}=19$ (Total Evidence analysis) were used as in the analysis of Abdala et al. (2020). One thousand replications
were performed for each search. Symmetric resampling was used to obtain support values for the results obtained, with 500 replications with a deletion probability of 0.33 . To construct the cyt- $b$ tree, sequences from this study
( 13 species) were combined with a published dataset of 24 species, and five undescribed lineages of Liolaemus (Aguilar et al. 2016; Aguilar-Puntriano et al. 2018, 2019; Chaparro et al. 2020; De Gamboa et al. 2018; Olave et al. 2014; Villegas-Paredes et al. 2020) [Table 2]. A maximum likelihood phylogenetic analysis was carried out with MEGA X (Kumar et al. 2018). Heuristic tree searches were performed with the GTR $+\mathrm{G}+\mathrm{I}$ substitution model (determined based on the Akaike information criterion), and 1,000 bootstrap replications.

## Results and Discussion

The independent taxonomic status of the population of Liolaemus studied here was validated using morphological and molecular evidence. The results of the phylogenetic and statistical analyses described below suggest that the population can be considered as distinctive from all other described species of Liolaemus. In accordance with best practices in zoological nomenclature, the results of statistical, morphological, and molecular phylogenetic analyses are provided following the formal presentation of the new proposed species.

## Taxonomy

Liolaemus anqapuka Huamaní-Valderrama, Quiroz, Gutiérrez, Aguilar-Kirigin, Chaparro, Abdala sp. nov. (Figs. 2-5).
urn:Isid:zoobank.org:act:EF6ABFF4-97BC-4C8F-83E7-79D2B3FE7171
1885 Ctenoblepharis adspersus-Boulenger, Catalogue of the Lizards in the British Museum (Natural History). Second Edition 2: 136-137.
1978b "Ctenoblepharus sp." Péfaur et al. Bulletin de l'Institut Français d'Études Andines VII (1-2): 129-139. 1982 Liolaemus insolitus Cei and Péfaur, In Actas 8vo Congreso Latinoamericano de Zoología. Pp. 573-686.
1995 Ctenoblepharys adspersa-Etheridge, American Museum Novitates 3142: 1-34.
2004 Phrynosaura [sp.] Nuñez, Noticiario Mensual Museo de Historia Natural 353: 28-34.
2010 Liolaemus cf. insolitus, Gutierrez and Quiroz, Herpetofauna del Sur del Perú, Available: http:// herpetofaunadelsurdelperu.blogspot.com [Accessed: 13 June 2020].
2011 Liolaemus species 2, Langstroth, Zootaxa 2809: 32. 2020 Liolaemus aff. insolitus7, Abdala et al., Zoological Journal of the Linnean Society 189: 1-29.

Holotype. MUSA 5573, an adult male (Figs. 2-3), from between Quebrada San Jose and Quebrada Tinajones, District of Uchumayo, Province of Arequipa, Department of Arequipa, Peru ( $16^{\circ} 31^{\prime} 47^{\prime \prime} \mathrm{S}, 71^{\circ} 39^{\prime} 04^{\prime \prime} \mathrm{W}$ ) at $2,460 \mathrm{~m}$ asl, collected on 10 November 2013, by C.S. Abdala, R. Gutiérrez, A. Quiroz, L. Huamani, and J. Cerdeña.

Paratypes. Six adult females: MUSA 5574-75, same data as holotype. MUSA 1766, from Quebrada Tinajones, 300 m southeast of holotype ( $16^{\circ} 31^{\prime} 54.29^{\prime \prime} \mathrm{S}$, $71^{\circ} 38^{\prime} 57.547^{\prime \prime} \mathrm{W}$ ) at $2,492 \mathrm{~m}$ asl, collected on 9 October 2010, by A. Quiroz and J. Cerdeña. MUBI 13522, MUSA 1767, from Quebrada Tinajones, 600 m southeast of holotype ( $16^{\circ} 31^{\prime} 54.207^{\prime \prime} \mathrm{S}, 71^{\circ} 38^{\prime} 46.187^{\prime \prime} \mathrm{W}$ ) at 2,528 m asl, collected on 9 October 2010, by A. Quiroz and J. Cerdeña. MUBI 14680, from Quebrada Tinajones $\left(6^{\circ} 31^{\prime} 22.705^{\prime \prime} \mathrm{S}, 71^{\circ} 37^{\prime} 35.666^{\prime \prime} \mathrm{W}\right)$ at $2,561 \mathrm{~m}$ asl, collected on 27 July 2007, by R. Gutiérrez and A. Quiroz. Two adult males: MUBI 13521, from Quebrada Tinajones, 300 m southeast of holotype ( $16^{\circ} 31^{\prime} 54.29^{\prime \prime} \mathrm{S}$, $71^{\circ} 38^{\prime} 57.547^{\prime \prime} \mathrm{W}$ ) at $2,492 \mathrm{~m}$ asl, collected on 9 October 2010, by A. Quiroz and J. Cerdeña. MUBI 14417, from Quebrada Tinajones ( $16^{\circ} 31^{\prime} 22.705^{\prime \prime} \mathrm{S}, 71^{\circ} 37^{\prime} 35.666^{\prime \prime} \mathrm{W}$ ) at $2,561 \mathrm{~m}$ asl, collected on 27 July 2007, by R. Gutiérrez and A. Quiroz.

Diagnosis. We assign Liolaemus anqapuka sp. nov. to the $L$. montanus group because it presents a blade-like process on the tibia, associated with the hypertrophy of the tibial muscle tibialis anterior (Abdala et al. 2020; Etheridge 1995) and its placement in the morphological and molecular phylogenies (Fig. 11). Within the $L$. montanus group, Liolaemus anqapuka sp. nov. differs from $L$. andinus, $L$. annectens, $L$. aymararum, $L$. cazianiae, L. chlorostictus, L. dorbignyi, L. fabiani, L, forsteri, L. foxi, L. gracielae, L. huayra, L. inti, L. jamesi, L. melanogaster, L. multicolor, L. nigriceps, L. orientalis, L. pachecoi, L. pantherimus, L. patriciaiturrae, L. pleopholis, L. polystictus, L. puritamensis, L. qalaywa, L. robustus, L. scrocchii, L. signifer, L. vallecurensis, L. victormoralesii, L. vulcanus, and $L$. williamsi, for being species of larger size (SVL greater than 75 mm ) unlike L. anqapuka sp. nov., which has a maximum SVL of 73.5 mm . Liolaemus anqapuka sp. nov., has between 58 and 72 (mean $=64.8$ ) scales around the body, which differentiates it from species of the group with more than 80 scales, such as L. cazianiae, L. duellmani, L. eleodori, L. erguetae, L. forsteri, L. gracielae, L. molinai, L. multicolor, L. nigriceps, L. patriciaiturrae, L. pleopholis, L. poecilochromus, L. porosus, L. pulcherrimus, L. robertoi, L. rosenmanni, L. ruibali, and L. vallecurensis, and also from species with less than 55 scales, like $L$. aymararum, L. jamesi, L. pachecoi, and L. thomasi. Liolaemus anqapuka sp. nov. have 60-72 dorsal scales (mean $=65.5$ ), and differs from L. andinus, L. cazianiae, L. eleodori, L. erguetae, L. forsteri, L. foxi, L. gracielae, L. halonastes, L. molinai, L. multicolor, L. nigriceps, L. patriciaiturrae, L. pleophlolis, L. poecilochromus, L. porosus, L. pulcherrimus, L. robertoi, L. rosenmanni, L. ruibali, L. schmidti, and $L$. vallecurensis, which have between $75-102$ dorsal scales. The number of ventral scales between 73-87 (mean $=81.3$ ) differentiates it from species with more than 90 ventral scales, such as $L$. andinus, L. cazianiae, L. erguetae, L. eleodori, L. foxi, L.


Fig. 2. Details of the holotype of Liolaemus anqapuka sp. nov. (MUSA 5573; SVL $=73.5 \mathrm{~mm}$, Tail $=63.9 \mathrm{~mm}$ ): (A) dorsal and (B) ventral views of body; (C) ventral, (D) dorsal, and $\mathbf{( E )}$ lateral views of head; $\mathbf{( F )}$ ventral view of precloacal pores. Scale $=10 \mathrm{~mm}$.


Fig. 3. Adult male of the holotype, Liolaemus anqapuka sp. nov. (MUSA 5573; SVL $=73.5 \mathrm{~mm}$, Tail $=63.9 \mathrm{~mm}$ ), from the Department of Arequipa, 2,460 m asl. Photos by C.S. Abdala.
gracielae, L. halonastes, L. hajeki, L. molinai, L. nigriceps, L. patriciaiturrae, L. pleopholis, L. poecilochromus, L. porosus, L. robertoi, L. rosenmanni, and L. vallecurensis. Liolaemus anqapuka sp. nov. has juxtaposed or subimbricate dorsal scales, without keel or mucron, this differentiates it from species with conspicuous keel and mucron, as L. aymararum, L. etheridgei, L. famatinae, L. fittkaui, L. griseus, L. huacahuasicus, L. montanus, L. orko, L. ortizi, L. polystictus, L. pulcherrimus, L.qalaywa, L. signifer, L. tajzara, L. thomasi, L. victormoralesii, and L. williamsi. Females of $L$. anqapuka sp. nov. present 1-4 (mean $=2.6$ ) precloacal pores, this character differentiates it from species like L. andinus, L. balagueri, L. fitkaui, L. multicolor, L. ortizi, L. polystictus, L. puritamensis, L. robertoi, L. robustus, L. rosenmanni, L. ruibali, L. thomasi, and $L$. vallecurensis, because they do not present precloacal pores in females.

Liolaemus anqapuka sp. nov. belongs to the clade of Liolaemus reichei sensu Abdala et al. (2020). The color pattern of Liolaemus anqapuka sp. nov. has a combination of characteristics in males and females that distinguish it from the rest of the Liolaemus of the group. The number of scales around the body is between 58-72 ( mean $=64.8$ ), which differentiates it from L. audituvelatus, L. balagueri, L. insolitus, and L. reichei (Table 3). The number of dorsal scales varies between $60-72$ ( mean $=65.5$ ), which is lower than the number in $L$. audituvelatus, higher than in L. nazca, and has a variation in range of scales different than L. chiribaya, L. reichei, and L. torresi (Table 3). The numbers of ventral scales of Liolaemus anqapuka sp.
nov. vary between 73-87 (mean =81) which are different from $L$. audituvelatus, $L$. nazca, and $L$. torresi (Table 3). The presence of precloacal pores in females $1-4$ (mean $=$ 2.6), is different from L. audituvelatus, L. balagueri, and L. reichei, whose females do not have precloacal pores (Table 3). Coloration patterns on lateral sides have light blue scales, which are different from $L$. audituvelatus, $L$. balagueri, L. nazca, L. torresi, and L. reichei (Table 3). The existence of dorsal body scales with a keel differentiate it from L. nazca which have dorsal body scales without keel. Ventral thigh scales with keel are present in $100 \%$ of individuals of $L$. anqapuka $\mathbf{~ s p}$. nov. but they are less evident than those present in L. chiribaya, where only $35 \%$ of individuals present this character (Table 3). The maximum SVL is greater than in $L$. audituvelatus, $L$. poconchilensis, L. reichei, L. stolzmanni, and L. torresi (Table 3).

Description of the holotype (Figs. 2-3). Adult male (MUSA 5573), SVL 73.53 mm . Head 1.20 times greater in length ( 16.47 mm ) than width ( 13.74 mm ). Head height 10.48 mm . Neck width 14.37 mm . Eye diameter 3.67 mm . Interorbital distance 10.96 mm . Orbit-auditory meatus distance 6.55 mm . Auditory meatus 2.0 mm high, 0.97 mm wide. Orbit-commissure of mouth distance 5.77 mm . Internasal width 1.58 mm . Subocular scale length 4.09 mm . Trunk length 31.81 mm , width 24.37 mm . Tail length 63.91 mm . Femur length 14.65 mm , tibia 14.47 mm , and foot 18.01 mm . Humerus length 11.01 mm . Forearm length 9.31 mm . Hand length 10.82 mm . Pygal


Fig. 4. Male specimens of the Liolaemus anqapuka sp. nov. Photos by A. Quiroz (A-D) and C.S. Abdala (E).
region length 5.95 mm , and cloacal region width 7.97 mm . Dorsal surface of head rough, with 17 scales, rostral 3.09 times longer ( 2.78 mm ) than wide ( 0.9 mm ). Mental as long ( 2.78 mm ) as rostral, trapezoidal, surrounded by four scales. Nasal separated from rostral by one scale. Two internasals slightly longer than wide. Nasal surrounded by eight scales, separated from canthal by two scales. Nine scales between frontal and rostral. Frontals divided into three scales. Interparietal smaller than parietal, in contact with six scales. Preocular separated from lorilabials by one scale. Five superciliaries and 15 upper ciliaries scales. Three differential scales at anterior margin of auditory
meatus. Ten temporary scales. Four lorilabials scales, in contact with subocular. Seven supralabials, which are not in contact with subocular. Five supraocular. Eight lorilabials. Six infralabials. Five chin shields, $4^{\text {th }}$ pair separated by five scales. Seventy scales around half a body.

Sixty-two rounded dorsal body scales, juxtaposed, and without a keel or mucron; laminar anterior on members, imbricate and slightly keeled; laminar on hind limbs, imbricate and slightly keeled; tail with dorsal scales in the first third juxtaposed, and the remaining two-thirds imbricate, presence of some scales keeled. Eighty-six


Fig. 5. Female specimens of the Liolaemus anqapuka sp. nov. Photos by A. Quiroz.
ventral scales, from the mental to the cloacal region, following the ventral midline of the body, laminar, imbricated. Thirty-two imbricate gulars, smooth. Neck with longitudinal fold with 36 granular, not keeled scales, ear fold and antehumeral fold present. Gular fold incomplete. Forelimbs ventrally laminar, subimbricate to imbricate, not keeled; hind legs laminar, imbricate, with some keeled scales (Figs. 2-3). Seventeen subdigital lamellae on the $4^{\text {th }}$ finger of the hand. Twenty-one subdigital lamellae of the $4^{\text {th }}$ toe, with four keels, plantar scales with keels and mucrons. Lamellar ventral scales on tail, imbricate, not keeled. Five precloacal pores. Supernumerary pores absent.

Color of holotype in life (Fig. 3). Dorsal and lateral color of the neck is light gray with few light blue scales, with dull orange scales, and spots on side. Dorsum, limbs, and tail light gray. Vertebral region delimited, vertebral line and spots absent, but dotted with sky blue scales. Paravertebral and dorsolateral region of the body, large orange spots of irregular shape and size stand out. These orange spots are surrounded and dotted with numerous sky-blue scales, with thin design or undulating edges. The orange spots with light white irregular spots. There are no dorsolateral bands, antehumeral arch, or scapular spots. On the sides of the body the pattern of orange spots and
light blue scales is repeated, but the gray color of the body is darker. This design extends to the first third of the tail. Tail with dark semi-complete rings with white back spots. Midline of the body with orange scales and spots. Back of the limbs with numerous light white spots unevenly distributed. Hands and feet dorsally white. Ventrally white from mental region to the tail. Gular and femoral regions light yellow. Flanks of the body with a thin orange border from the armpits to the groin.

Morphological variation. Twenty-two specimens (six males and 16 females). Dorsal surface of head rough with $14-21$ scales (mean $=16.82 ;$ STD $=1.71$ ). Nasal surrounded by 6-9 scales (mean $=7.41 ; \mathrm{STD}=0.73$ ). Supralabials $7-10$ scales (mean $=8.18 ;$ STD $=0.8$ ), lorilabials $8-11$ scales (mean $=9.32 ; \mathrm{STD}=0.89$ ). A line of lorilabial scales. Supraoculars $4-6$ ( mean $=5.45$; STD $=0.6$ ). Interparietals smaller than parietals, surrounded by $4-8$ scales (mean $=6.32 ;$ STD $=1.09$ ). Infralabials 6-9 (mean $=7.14 ;$ STD $=0.77$ ). Gulars 28-39 (mean $=33.41$; STD $=2.99$ ). Temporals smooth, $7-10$ scales (mean $=$ $9.09 ; \mathrm{STD}=0.97$ ). Meatus auditory higher $1.37-2.47 \mathrm{~mm}$ (mean $=2.05 ; \mathrm{STD}=0.26$ ), than wide $0.20-1.20$ (mean $=0.81 ; \mathrm{STD}=0.25$ ). Head longer 12.32-17.20 (mean $=$ $14.91 ; \mathrm{STD}=1.31)$ than wide $9.15-15.92($ mean $=12.77$; $\mathrm{STD}=2.03$ ). Head height $6.84-10.48$ ( mean $=8.38$; STD
Table 3. Differences in morphological characters of the Liolaemus reichei clade.

| Morphological character | L. auditvetulaus | L. balagueri | L. reichei | L. insolitus | L. poconchilensis | L. torresi | L. chiribaya | L. nazca | L. anqapuka sp. nov. |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | ( $n=4$ ) | ( $n=18$ ) | ( $n=3$ ) | $(n=10)$ | ( $n=4$ ) | ( $n=8$ ) | ( $n=10$ ) | ( $n=7$ ) | ( $n=22$ ) |
| Snout-vent length | 47.2 (47.5) 47.8 | $50.9(59.1) 66.5$ | 41.5 (47.7) 50.8 | 50.3 (59.4) 65.6 | 47.17 (51.7) 53.83 | $53.8(58.1) 64$ | $\begin{gathered} 49.28(59.60) \\ 68.25 \end{gathered}$ | $\begin{gathered} 53.51(59.35) \\ 64.34 \end{gathered}$ | $\begin{gathered} 52.15 \text { (63.92) } \\ 73.53 \end{gathered}$ |
| Tail length | 45.3 (46.3) 47.5 | 48.7 (59.4) 80.0 | 35.7 (39.5) 43.1 | 45.4 (51.7) 61.9 | 42.66 (47.2) 53.65 | $58.8(57.4) 74$ | $\begin{gathered} 46.34 \text { (56.47) } \\ 68.89 \end{gathered}$ | $\begin{gathered} 60.26 \text { (70.55) } \\ 79.60 \end{gathered}$ | $\begin{gathered} 46.77(56.83) \\ 67.16 \end{gathered}$ |
| Snout-vent length/ Tail length | 0.95 (0.98) 1.01 | 0.93 (1.02) 1.09 | - | 0.82 (0.91) 0.98 | - | - | 0.89 (0.98) 1.07 | - | 0.76 (0.90) 1.05 |
| Head length | 11.4 (11.6) 11.7 | $12.4(14.1) 17.1$ | $10(10.9) 11.5$ | $11.6(13.6) 14.9$ | 11.34 (13.1) 14.16 | 13 (13.6) 14.5 | $\begin{gathered} 12.18 \text { (14.00) } \\ 15.63 \end{gathered}$ | $\begin{gathered} 12.82(14.35) \\ 16.46 \end{gathered}$ | 12.32 (14.90) 17.2 |
| Head width | $9.6(9.8) 10.3$ | $9.8(11.2) 13.6$ | 8.3 (8.5) 9.7 | 9.5 (11.5) 12.4 | 9.51 (10.9) 11.53 | 10.3 (11.0) 11.7 | 8.92 (10.29) 11.44 | 8.99 (10.12) 11.74 | 9.15 (12.76) 15.92 |
| Forelimb length | 27.1 (28.6) 28.7 | $21.0(22.9) 25.1$ | 21.4 (22.6) 24.4 | 26.1 (29.1) 31.5 | 22.2 (24.8) 27.5 | 26.3 (28.8) 30.5 | $\begin{gathered} 25.17(28.41) \\ 29.87 \end{gathered}$ | $19.22(23.10)$ | $\begin{gathered} 25.68(28.71) \\ 31.53 \end{gathered}$ |
| Hind limb length | 37.1 (38.8) 40.6 | 29.1 (32.4) 35.9 | 30.1 (31.7) 33.4 | 37.4 (41.2) 44.3 | 31.15 (34.1) 32.62 | 38.6 (40.1) 42.2 | $\begin{gathered} 36.13(39.79) \\ 42.68 \end{gathered}$ | $\begin{gathered} 32.05(35.06) \\ 37.92 \end{gathered}$ | $\begin{gathered} 36.02(41.28) \\ 47.13 \end{gathered}$ |
| Lorilabials scales | 7 (8) 9 | $5(6.9) 8$ | 8 (8.7) 9 | 7 (8.2) 10 | 14 | $8(8.4) 9$ | 5 (5.5) 6 | 7 (8.4) 10 | $8(9.32) 11$ |
| Auditory meatus scales | 0 | 1 | 1 | $1(1.5) 3$ | 1 (2) 3 | 1 | 1 | $1(1.86) 2$ | $1(1.55) 3$ |
| Upper ear scale | 0 (1) 2 | 0 | 0 | 1 | $0(0.75) 1$ | 0 | $0(0.85) 1$ | 1 | 1 |
| Diagonal large atrial scale | $00.5) 1$ | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Neck scales | 45 (45) 45 | 29 (31) 38 | 26 (28.7) 33 | 35 (36.7) 38 | 35 (36.5) 38 | 44 (45.9) 47 | 28 (28.4) 32 | 28 (30.86) 32 | $32(38.86) 43$ |
| Scales around midbody | 74 (74.5) 75 | $52(54.0) 56$ | 43 (45) 47 | 51 (55.4) 58 | 57 (59.4) 62 | 64 (66.6) 72 | 55 (61.8) 66 | 53 (56) 60 | 58 (65.09) 72 |
| Dorsal scales | 78 (82.5) 87 | $50(55.1) 68$ | 50 (51.7) 54 | $56(62.9) 68$ | 57 (61.2) 64 | 70 (74.4) 80 | 52 (57.4) 61 | 53 (54.14) 56 | $60(65.59) 72$ |
| Ventral scales | 86 (90.5) 95 | 65 (73.4) 79 | 80 (86.4) 88 | 70 (73.9) 78 | 77 (79.6) 84 | 86 (90.6) 97 | 67 (72.7) 77 | 65 (70.57) 74 | 73 (81.32) 87 |
| Dorsal scale arrangement of the body | Juxtaposed and sub-juxtaposed | Sub-juxtaposed | Juxtaposed | Sub-juxtaposed and Imbricated | Juxtaposed and imbricated | Juxtaposed | Juxtaposed and sub-juxtaposed | Imbricadas | Juxtaposed |
| Keel scales | absent | absent | absent | absent | absent | absent | absent | present | absent |
| Percentage of individuals with ventral keel scales in the center of the thigh | 0\% | 0\% | 0\% | 0\% | 0\% | 0\% | 35\% | 0\% | 100\% |

Table 3 (continued). Differences in morphological characters of the Liolaemus reichei clade.

| Morphological character | L. auditvetulaus | L. balagueri | L. reichei | L. insolitus | L. poconchilensis | L. torresi | L. chiribaya | L. nazca | L. anqapuka sp. nov. |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Arrangement of celestial scales in males | absent | absent | absent | Regular, from the occiput to approximately two thirds of the tail | Both sides of the body | absent | Regular, associated with paravertebral and lateral | absent | Light blue scales that can form thin irregular lines or clump together forming conspicuous spots |
| Arrangement of celestial scales in females | absent | absent | absent | Scales, next to paravertebral spots | absent | absent | absent | absent | Sometimes light blue lateral scales on paravertebral spots |
| Green side spots | absent | present | absent | absent | absent | absent | absent | present | absent |
| Precloacal pores in females | 0 | 0 | 0 | $0(1.3) 3$ | $0(1.3) 2$ | $0(1.5) 2$ | 2 (3) 4 | 1 (2) 3 | $3(4.22) 5$ |
| Precloacal pores in males | 5 | 3 (5.08) 7 | 4 | $5(6.2) 7$ | $4(4.6) 5$ | 3 | $3(4.14) 6$ | 3 (4) 6 | $4(5) 6$ |

$=0.87$ ). Underarm to groin length 21.61-32.8 (mean $=$ 28.58 ; STD $=2.76$ ). SVL males $56.23-73.53 \mathrm{~mm}$ (mean $=65.05 \mathrm{~mm} ; \mathrm{STD}=7.08$ ) and females $52.15-71.10 \mathrm{~mm}$ (mean $=62.9 \mathrm{~mm} ; \mathrm{STD}=4.61$ ). Femur length $10.11-14.65$ mm (mean $=12.31 \mathrm{~mm} ; \mathrm{STD}=1.06$ ). Humerus length $7.56-11.01 \mathrm{~mm}$ (mean $=8.86 \mathrm{~mm} ; \mathrm{STD}=0.99$ ). Forearm length $7.65-11.56 \mathrm{~mm}$ (mean $=9.59 \mathrm{~mm} ; \mathrm{STD}=1.06$ ). Hand length 8.03-11.25 (mean $=10.25 ;$ STD $=0.86)$. Scales around midbody 58-72 ( mean $=65.09$; STD $=3.7$ ). Dorsal $60-72$ (mean $=65.59 ; \mathrm{STD}=3.5$ ), juxtaposed to sub-juxtaposed, and smooth scales. Infradigital lamellae of the $4^{\text {hh }}$ finger of the hand 15-21 ( mean $=17.73$; STD $=1.45)$ and of the $4^{\text {th }}$ toe $20-26($ mean $=21.67 ;$ STD $=$ 1.5). Ventral $73-87($ mean $=81.32 ; \mathrm{STD}=3.37$ ) larger than dorsal scales. Tail length $46.77-67.16 \mathrm{~mm}(n=17$, mean $=56.83 \mathrm{~mm} ;$ STD $=5.91$ ). Males with 4-6 (mean $=4.67$; $\mathrm{STD}=0.82$ ) precloacal pores, and females with $3-5$ (mean $=4.22 ;$ STD $=0.83$ ) precloacal pores. Body measurements, males ( mean $=66.62 \mathrm{~mm}$ ) slightly larger than females (mean $=62.90 \mathrm{~mm}$ ), tail length in males slightly larger $($ mean $=61.74 \mathrm{~mm})$ than females $($ mean $=$ 54.80 mm ) [Table 4].

Color variation in life (Figs. 4-5). Liolaemus anqapuka sp. nov. shows evident sexual dichromatism. In males, head is darker than the gray body. In some specimens, supralabial and infralabial scales are generally lighter gray than the rest of the head. The subocular is generally white with irregular dark spots. The dorsal color of the neck is gray, varying in its hue, and may be dotted with some light blue scales and orange spots. The body color is always gray. The vertebral region in most males is well delimited with some light blue scales. No vertebral line, dorsolateral bands, antehumeral arch, or scapular spots. Few specimens have diffuse gray paravertebral spots, and rounded shape. As in the holotype, in the paravertebral, dorsolateral, and lateral regions of the body, irregular orange spots stand out, surrounded and dotted with celestial scales. Orange spots can vary in intensity and size, as light blue scales that can form thin irregular lines or clump together to form more conspicuous spots. In some specimens the amount of light blue scales is so remarkable that they cover the orange spots. Orange spots and light blue scales are distributed on the sides of the tail. In some individuals, the celestial scales reach the distal end of the tail. In some specimens, light blue scales are replaced by dark, bluish-green scales. In some, irregularly shaped white spots are distributed among the orange spots. The fore and hind limbs, as well as the tail, have the same design as the body. In the tail, incomplete rings of dark spots with light edges are formed. Ventrally, the majority of males are similar. The predominant color is white, some have faint yellow and a yellow hue that can vary in intensity, highlighted in the gular region and the hind limbs. On the sides of the belly, a thin orange longitudinal line protrudes from the armpit to the groin (Fig. 4).

Table 4. Differences in morphological characters between males and females of Liolaemus anqapuka sp. nov.

| Morphological characters | Mean in <br> males | STD <br> males | Variation in <br> males | Mean in <br> females | STD <br> females | Variation in <br> females |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| Snout-vent length | 66.62 | 6.05 | $(56.23-73.53)$ | 62.91 | 4.61 | $(52.15-71.10)$ |
| Tail length | 61.74 | 3.74 | $(58.08-67.16)$ | 54.78 | 5.49 | $(46.77-66.88)$ |
| Head length | 15.9 | 0.85 | $(14.87-17.2)$ | 14.53 | 1.27 | $(12.32-16.79)$ |
| Head width | 13.94 | 1.46 | $(11.5-15.92)$ | 12.33 | 2.08 | $(9.15-15.38)$ |
| Forelimb length | 30.45 | 0.77 | $(29.41-31.53)$ | 28.05 | 1.58 | $(25.68-31.36)$ |
| Hind limb length | 44.03 | 2.33 | $(39.99-47.13)$ | 40.25 | 2.9 | $(36.02-45.04)$ |
| Head length/snout-vent length | 0.24 | 0.02 | $(0.22-0.26)$ | 0.23 | 0.01 | $(0.21-0.25)$ |
| Head length/head width | 1.15 | 0.09 | $(1.04-1.29)$ | 1.2 | 0.13 | $(1.02-1.37)$ |
| Trunk width/trunk length | 0.7 | 0.06 | $(0.64-0.78)$ | 0.69 | 0.1 | $(0.53-0.97)$ |
| Tympanum height/tympanum width | 2.74 | 1.07 | $(2.06-4.9)$ | 3.08 | 2.21 | $(1.57-10.7)$ |
| Auditory meatus scales | 1.5 | 0.55 | $(1-2)$ | 1.56 | 0.63 | $(1-3)$ |
| Neck scales | 39.33 | 3.5 | $(34-42)$ | 38.7 | 3.91 | $(32-43)$ |
| Scales around midbody | 65.67 | 4.59 | $(60-72)$ | 64.9 | 3.46 | $(58-72)$ |
| Dorsal scales | 67.17 | 4.58 | $(61-72)$ | 65 | 2.97 | $(60-72)$ |
| Ventral scales | 83.5 | 2.51 | $(81-87)$ | 80.5 | 3.35 | $(73-84)$ |
| Pygal scales | 6.5 | 2.07 | $(5-10)$ | 6.75 | 1.69 | $(5-10)$ |
| Precloacal pores | 4.67 | 0.82 | $(4-6)$ | 3.64 | 1.15 | $(2-5)$ |

Females have a totally different coloring pattern than males (Fig. 5). The color of the head varies from brown to gray, with some dark red spots and scales. The supralabial, infralabial, and lorilabial scales are lighter in color than the dorsal surface of the head. The back of the body can be light gray or brown; with small paravertebral spots, gray or dark brown, and circular or sub-quadrangular; with a small white spot on the back which can be the same size as the paravertebral; and with meager orange spots between the paravertebrals. A few females have light blue scales on paravertebral spots. On the sides of the body, there may be lateral spots of the same design as the paravertebral ones. The tail and hind limbs have the same design and color as the body, without dorsolateral bands. Ventrally they are white or faint yellow immaculate throughout the body. In some females, the tail has more intense yellow throughout its extension (Fig. 5).

Etymology. The specific name refers to the coloration patterns of males. The word "anqapuka" is an original word in the Quechua language (spoken currently in the Peruvian Andes), corresponding to a complex word between "anqa" assigned to the blue color, and "puka" which means orange or red color.

Distribution and natural history. Liolaemus anqapuka sp nov. is restricted to the western slopes of the La Caldera batholith, Arequipa, Peru, between 1,800 and $2,756 \mathrm{~m}$ asl, which includes the upper altitude limit of the La Joya desert (Fig. 6). The distribution is within the Desert biogeographic province (sensu Morrone 2014). Liolaemus anqapuka sp. nov. inhabits arid
environments, characteristic of the desert of southern Peru, with sandy-stony substrates and little slope, seasonal herbaceous vegetation, and columnar and prostrate cacti. This species also inhabits sectors without vegetation (Fig. 7). It takes refuge mainly under stones, and in burrows that surround the roots of small bushes, prostrate cacti, and in cavities underground or in hardened sand. Some specimens of Liolaemus anqapuka sp. nov. were observed feeding on coleopteran larvae, as well as larvae and notably adults of Lepidoptera belonging to the Sphingidae family (Fig. 8). Feeding on beetles is very similar to that reported for the closelyrelated species Liolaemus insolitus, which is specialized in feeding on so-called "flea beetles" of the subfamily Halticinae (Coleoptera: Chrysomelidae) [Cei and Péfaur 1982]. The adults and larvae of the family Sphingidae are most abundant in the summer months, when the local rainfall is complemented by abundant ephemeral surface watercourses whose flow is derived from rainfall on the western slopes of the Andes, and these insects can display unusual and explosive development. During years when there is exceptionally high accumulated rainfall, a biological phenomenon known as a "blooming desert" can occur (Chavez et al. 2019), and some phytophagous insects would be expected to be able to use the abundant plant resources that suddenly become available in these events, as reported for Sphingidae in northern Chile (Vargas and Hundsdoerfer 2019). Liolaemus anqapuka sp. nov. was found in syntopy with other reptile species, such as Microlophus sp. and Phyllodactylus gerrhopygus.

Endemism, threats, and conservation status. Liolaemus anqapuka sp. nov. is considered as an endemic species


Fig. 6. Geographic distribution of Liolaemus montanus group species from Peru. Symbols with a black dot in the middle represent the type locality of each species. Species with quotation marks in the names belong to the candidate species listed in Aguilar et al. (2016).
with a restricted-range of geographical distribution, because the species occupancy is less than $10,000 \mathrm{~km}^{2}$ (Bruchmann and Hobohm 2014; IUCN 2016; Kier and Barthlott 2001; Noguera-Urbano 2017). Using the Geocat tool, and based on records of the species, we estimate the extent of occurrence (EOO) at $147.2 \mathrm{~km}^{2}$ and the area of occupancy (AOO) at $80.0 \mathrm{~km}^{2}$. The restricted range might be caused by their climatic tolerance, and the ecological adaptation to extreme environmental conditions found on the Desert biogeographic province. The main threats are the loss of habitat, because of the large-scale mining activities, urban expansion, and contamination by chemicals and metals; and also because of the presence of highways that cut through their natural habitat, and the opening of new secondary roads. Following the IUCN (2020) criteria, and using the actual knowledge of the new species, we evaluated the conservation status of $L$. anqapuka sp. nov. to be in the category of endangered EN [A2cde; A3cde; A4cde] [B1ab (i, iii) + 2abc (ii, iii, iv)], based on the area of occupancy $(\mathrm{AOO})<500 \mathrm{~km}^{2}$, the extent of occurrence $(\mathrm{EOO})<5,000 \mathrm{~km}^{2}$, the number of localities are $\leq 5$; and we consider it as a species with restricted range because $L$. anqapuka sp. nov. has a global range size less than or equal to $10,000 \mathrm{~km}^{2}$ (IUCN 2016).

Statistical analysis (Figs. 9-10). The summary statistics for all the non-transformed, continuous, and meristic characters taken from five species of Liolaemus are shown in Appendix II. The homogeneity of variance was not supported for either continuous or meristic characters by the Levene's test in some groups. Therefore, the results of the Principal Component Analyses (PCA) should be preferred for deriving linear combinations of the variables that summarize the variation in the data set. The results of the PCA for continuous and meristic characters are presented separately (Tables 5-6).

The first four components of continuous characters explained $55.51 \%$ of the variation, and a screen plot test of the PCs indicated that only the first three components contained nontrivial information. The first axis represents body size, loading negatively for most variables, and accounts for $23.46 \%$ of the variation, with strong loading for width of the base of the tail. The second axis represents morphological variation and accounts for most of the remaining variation, with strong loadings for mental scale width, length of the $4^{\text {th }}$ supralabial scale, and upper width of the pygal area. The next axes account for the remaining variation.

The first four components of meristic characters explained $54.59 \%$ of the variation, and a screen plot

Table 5. Principal component (PC) axes loadings of continuous characters for L. balagueri ( $n=12$ ), L. chiribaya ( $n=10$ ), $L$. insolitus ( $n=15$ ), L. nazca ( $n=7$ ), and Liolaemus anqapuka sp. nov. $(n=7$ ). Eigenvectors, eigenvalues, and percentage of variance explained for the first four principal components from transformed data in the five putative species of Liolaemus.

| Loadings | PC1 | PC2 | PC3 | PC4 |
| :--- | :---: | :---: | :---: | :---: |
| Percentage variation accounted for | 23.46 | 14.84 | 10.97 | 6.24 |
| Eigenvalue | 7.27 | 4.6 | 3.4 | 1.93 |
| Snout-vent length | -0.85 | -0.06 | 0.09 | 0.16 |
| Minimum distance between the nasal scales | -0.13 | 0.48 | 0.67 | -0.02 |
| Snout width at the edge of the flake canthal | -0.04 | 0.2 | 0.54 | 0.2 |
| Distance from the nose to the back edge of the flake canthal | -0.68 | -0.08 | -0.15 | 0.08 |
| Distance between the posterior edge of the series superciliary | -0.67 | 0.56 | 0.01 | 0.23 |
| Length of the interparietal | -0.48 | 0.08 | -0.44 | -0.29 |
| Length of the parietal | -0.51 | 0.43 | -0.20 | -0.27 |
| Mental flake width | 0.13 | 0.73 | 0.49 | 0.05 |
| Length of the mental scale | -0.50 | -0.33 | -0.68 | -0.16 |
| Distance from nostril to the mouth | -0.55 | -0.43 | 0.28 | 0.01 |
| Rostral height | -0.51 | -0.19 | 0.16 | 0.05 |
| Length of the subocular scale | -0.41 | -0.19 | 0.01 | 0.06 |
| Ear height | -0.16 | -0.23 | 0.22 | -0.49 |
| Ear width | 0.11 | 0.29 | 0.67 | -0.32 |
| Length of the preocular scales | -0.11 | -0.56 | 0.19 | 0.14 |
| Preocular width | -0.26 | -0.46 | 0.32 | 0 |
| Length of the fourth supralabial flake | -0.25 | -0.71 | 0.17 | -0.17 |
| Length of the fourth lorilabial flake | -0.50 | -0.46 | 0.04 | 0.04 |
| Length between orbits | -0.61 | 0.37 | -0.05 | 0.46 |
| Length of the first finger of the forelimb, without the claw | -0.54 | 0.41 | -0.16 | -0.29 |
| Length of the claw of the fourth finger of the forelimb | -0.15 | 0.32 | -0.56 | 0.29 |
| Length of the fifth finger of the forelimb, without the claw | -0.19 | 0.17 | 0.23 | -0.68 |
| Humerus width | -0.62 | 0.06 | -0.03 | 0.24 |
| Distance from the insertion of the forelimb in the body toward the elbow | -0.67 | 0.17 | 0.29 | 0.12 |
| Thigh width | -0.66 | -0.50 | -0.01 | -0.23 |
| Length of the first finger of the hind limb, without the claw | -0.24 | 0.35 | -0.21 | -0.38 |
| Length of the claw of the fourth finger of the hind limb | -0.54 | 0.19 | -0.15 | -0.26 |
| Body width | -0.62 | -0.12 | 0.53 | -0.02 |
| Width of the base of the tail | -0.12 | 0.22 | 0.19 |  |
| Upper width of the pygal area | -0.11 | -0.13 |  |  |

test of the PCs indicated that only those components contain relevant information. The four axes represent morphological variation, loading strongly for number of paravertebral spots in the right side, number of scales around midbody, number of ventral scales, and number of gular scales. The four axes account for the remaining variation, albeit with values below 0.70 for subdigital lamellae of the $4^{\text {th }}$ finger of the forelimb, number of auricular scales, projecting scales on anterior edge of auditory meatus, and number of organs in the postrostral scales.

The positions of species based on their scores for the two morphological principal components axes are illustrated
in Figs. 9-10. The spatial distribution of the continuous characters indicates that they are sufficient to virtually separate the five Peruvian Liolaemus species of the $L$. reichei group. These species can also be distinguished by their position in the analysis of meristic characters only. In both analyses, Liolaemus anqapuka sp. nov. can be differentiated from other phylogenetically related species by its body size and morphological variation.

To further clarify the position of the Liolaemus species in the morphospace of both continuous and meristic characters, a DFA was carried out, where the group membership was determined a priori. The result obtained through the DFA for the five species of Liolaemus was

Table 6. Principal component (PC) axes loadings of meristic characters for L. balagueri ( $n=12$ ), L. chiribaya ( $n=10$ ), $L$. insolitus ( $n=15$ ), L. nazca $(n=7)$, and Liolaemus anqapuka sp. nov. $(n=7)$. Eigenvectors, eigenvalues, and percentage of variance explained for the first four principal components from transformed data in the putative species of Liolaemus.

| Loadings | PC1 | PC2 | PC3 | PC4 |
| :---: | :---: | :---: | :---: | :---: |
| Percentage variation accounted for | 26.62 | 10.3 | 9.63 | 8.04 |
| Eigenvalue | 8.78 | 3.4 | 3.18 | 2.65 |
| Number of scales around the interparietal scale | -0.06 | $-0.36$ | $-0.03$ | 0.05 |
| Supralabials number on the right side | -0.04 | -0.52 | $-0.27$ | 0.18 |
| Supralabials number on the left side | 0.17 | $-0.51$ | -0.47 | 0.42 |
| Infralabials number on the right side | 0.39 | -0.30 | $-0.44$ | $-0.01$ |
| Infralabials number on the left side | 0.25 | $-0.55$ | $-0.47$ | -0.07 |
| Number of scales around mental scale | 0.37 | -0.09 | 0 | $-0.11$ |
| Number of scales around the rostral scale | 0.56 | 0.31 | -0.26 | -0.40 |
| Number of lorilabials | -0.16 | -0.56 | 0.07 | -0.45 |
| Hellmich index | 0.32 | -0.10 | -0.39 | 0.4 |
| Subdigital lamellae of the first finger of the forelimb | -0.09 | -0.59 | 0.48 | -0.04 |
| Subdigital lamellae of the second finger of the forelimb | 0.06 | -0.35 | 0.47 | 0.44 |
| Subdigital lamellae of the third finger of the forelimb | -0.31 | $-0.07$ | 0.55 | 0.2 |
| Subdigital lamellae of the fourth finger of the forelimb | -0.74 | -0.12 | -0.14 | 0.24 |
| Subdigital lamellae of the fifth finger of the forelimb | -0.61 | 0.12 | 0.38 | -0.22 |
| Subdigital lamellae of the first toe of the hind limb | -0.43 | -0.37 | 0.04 | 0.14 |
| Subdigital lamellae of the second toe of the hind limb | -0.56 | -0.40 | 0.46 | -0.16 |
| Subdigital lamellae of the third toe of the hind limb | -0.47 | -0.26 | 0.14 | -0.13 |
| Subdigital lamellae of the fourth toe of the hind limb | -0.08 | -0.55 | 0.23 | -0.48 |
| Subdigital lamellae of the fifth toe of the hind limb | -0.19 | 0.22 | 0.19 | 0.52 |
| Number of dorsal scales between the occiput and the level of the anterior edge of the thigh | 0.43 | -0.51 | -0.40 | -0.18 |
| Precloacal number of pores | 0.29 | -0.24 | 0.11 | 0.5 |
| Number of scales between canthal and nasal | -0.60 | -0.41 | -0.15 | 0.36 |
| Number of scales around the nasal scale | -0.20 | -0.12 | -0.05 | -0.09 |
| Supraoculars number enlarged scale in the right side | 0.67 | -0.22 | 0.2 | -0.27 |
| Supraoculars number enlarged scale in the left side | 0.48 | -0.23 | 0.05 | -0.48 |
| Number of scales between canthal and nasal scales | 0.7 | -0.26 | 0.15 | -0.09 |
| Number of organs in the third lorilabial scale | $-0.08$ | -0.18 | 0.58 | 0.2 |
| Number of organs above the row of lorilabials scales and below the canthal and preocular scales | 0.66 | 0.02 | 0.34 | -0.13 |
| Gular number of scales | -0.88 | 0.01 | -0.27 | -0.25 |
| Number of scales around the middle body | -0.92 | 0 | -0.27 | -0.09 |
| Number of ventral scales | -0.92 | 0.03 | -0.26 | -0.15 |
| Number of auricular scales | -0.73 | 0.04 | -0.02 | -0.31 |
| Number of paravertebral spots in the right side | -0.93 | -0.02 | -0.23 | -0.10 |

not significant for continuous morphological characters (Wilk's Lambda $=0.85, F=0.71, P=0.60$ ), and the jackknife classification was $100 \%$ satisfactory. The DFA of operational taxonomic units for meristic characters was not significant either (Wilk's Lambda $=0.69, F=1.58, P$ $=0.23$ ); however, the jackknife satisfactory classification was developed at a $100 \%$ rate. These results show $L$. anqapuka sp. nov. can be reliably distinguished from
the other species by a combination of morphological characters.

Phylogenetic analysis (Fig. 11). The objective of the phylogenetic analyses carried out (morphological, molecular, and Total Evidence) is not to resolve the relationships of the L. montanus group, which is far beyond the scope of this study. The main objective of


Fig. 7. Habitat of Liolaemus anqapuka sp. nov. in (A) dry season and (B) wet season. Photos by A. Quiroz (A), C.S. Abdala (B).
these analyses is to obtain some approximation of the phylogenetic relationships of L. anqapuka sp. nov. and the rest of the $L$. reichei group sensu Abdala et al. (2020). The new taxon was recovered in three analyses, within the L. montanus group. In the morphological and Total Evidence analyses, under parsimony methodology, the $L$. reichei group is monophyletic; within this, L. anqapuka sp. nov., through molecular analysis of ML, the $L$. reichei group is paraphyletic.

Molecular analysis. The three DNA (cyt-b) obtained for L. anqapuka sp. nov. fall within the same clade, supporting the identification of the new species. The nearest terminal is $L$. aff. insolitus 4 , a population innominate from Department of Arequipa, and it is grouped in the same clade with L. chiribaya, a species from Department of Moquegua, with node support ( $\mathrm{BS}=99$ ). The clade that contains these three species is deeply separated from its sister clade, (L. poconchilensis + L. aff. insolitus8). The analysis does not recover the clade of $L$. reichei group sensu Abdala et al. (2020) as monophyletic.

Morphological analysis. The result of the morphological phylogenetic hypothesis shows that Liolaemus anqapuka sp. nov. belongs to the group of L. montanus, within the clade of L. reichei sensu Abdala et al. (2020), together with $L$. audituvelatus, L. balagueri, L. chiribaya, $L$. insolitus, L. nazca, L. poconchilensis, L. reichei, L. torresi, and eight unnamed populations so far. Liolaemus reichei sensu Abdala et al. (2020), is supported by 13 synapomorphies, of which four are continuous characters (lower number of scales from rostral to occiput, lower number of scales around midbody and lower ratio of tail length/SVL) and eight are discrete (ventral scales of the body equal to, or slightly larger than the dorsal; sides of the body not conspicuously colored, with little or no ventral sexual dichromatism; absence of white line in the temporal region; diameter of the eye, larger than the distance between the anterior margin of the eye, and the rostral scale; isognathic profile, substrate where they occur predominantly sandy).

This clade is divided into two large subclades, one with unnamed species and populations from Chile (L. audituvelatus, L. poconchilensis, L. reichei, and L. torresi) and the other with species and populations from central and southern Peru (L. balagueri, $L$. chiribaya, L. insolitus, and L. nazca). This last subkey is where the new species is recovered, supported by 19 synapomorphies, several of which stand out: ratio of auditory meatus height/head height, number of pygals, number of lorilabials contacting the subocular, number of supraoculars, dorsal surface of head (rugouse), scales on external edge of forelimbs (subimbricate), scales of dorsal hind limbs (subimbricate), with notch in edge of scales of gular fold, scales of pygal region (subimbricate), with dark line through the eye; white posterior edge of paravertebral spots in both sex (present), black dots scattered on dorsal region of hind limbs in males (absent), and dark line through the eye in females (present). Liolaemus anqapuka sp. nov. have populations of close relatives which also occur in Department of Arequipa, Peru, with particular morphological characteristics, and these are currently under description. Liolaemus anqapuka sp. nov. is recovered as a sister species of $L$. aff. insolitus 4 , a population related to $L$. insolitus near the


Fig. 8. Liolaemus anqapuka sp. nov. eating a moth of the Sphingidae family. Photo by A. Quiroz.


Fig. 9. Plot of principal component scores for continuous characters for L. balagueri (yellow stars, $n=12$ ), L. chiriba$y a$ (purple circles, $n=10$ ), L. insolitus (red triangles, $n=15$ ), L. nazca (sky blue triangle, $n=7$ ), and $L$. anqapuka sp. nov. (green squares, $n=7$ ). Eigenvectors, eigenvalues, and percent of variation explained for the first two principal components are summarized in Table 5.
coasts of the Department of Arequipa, which occupies elevations of $1,000 \mathrm{~m}$ asl. This relationship is supported by six synapomorphies. Liolaemus anqapuka sp. nov. is supported by seven autopomorphies in the phylogenetic tree (Fig. 11).

Total Evidence analysis (Fig. 11). The $L$. reichei clade is recovered as monophyletic, and $L$. anqapuka sp. nov. belongs to this clade, as do the sister species of $L$. aff. insolitus4, as well as in the morphological and molecular phylogenetics analyses. This relationship is supported by 14 synapomorphies, six of which are continuous characters and the support of this relationship is high ( $89 \%$ ). This relationship is recovered within the clade ( $L$. aff. insolitus5 (L. aff. insolitus $4+L$. anqapuka sp. nov.)), and is supported by three morphological and 11 molecular synapomorphies. Likewise, a total of seven autopomorphies support the new species of Liolaemus. In this hypothesis, as in the morphological one, two sub clades are recovered within the $L$. reichei clade-on the one hand are the species that are distributed in northern Chile, and on the other are those in southern Peru.

Taxonomic history. Boulenger (1885) identified a male specimen (BMNH 65-5-3-3) from "Arequiba, 7,500 ft" as Ctenoblepharis adspersus (an unjustified emendation of Ctenoblepharys adspersa Tschudi 1845) in his catalogue of the lizards in the British museum. Péfaur et al. (1978b) mentioned the distribution and classification of the reptiles from Department of Arequipa, noting that the specimens collected by Duellman (1974) from the "La Caldera batholith" located approximately 10 km southwest of Uchumayo town would be "Ctenoblepharus sp." (= Ctenoblepharys). But this was not the only mistake. Years later, Cei and Péfaur (1982) wrote the


Fig. 10. Plot of principal component scores for meristic characters for $L$. balagueri (yellow stars, $n=12$ ), L. chiribaya (purple circles, $n=10$ ), $L$. insolitus (red triangles, $n=15$ ), L. nazca (sky blue triangle, $n=7$ ), and $L$. anqapuka sp. nov. (green squares, $n=7$ ). Eigenvectors, eigenvalues, and percent of variation explained for the first two principal components are summarized in Table 6.
original description of Liolaemus insolitus, considered to be a widely distributed coastal species which reached altitudes above $2,000 \mathrm{~m}$ asl, including the populations of the "La Caldera batholith" from Department of Arequipa. Etheridge (1995), from the specimens considered by Boulenger (1885), identified the possible existence of a different species of Liolaemus from Department of Arequipa, which shows the characteristics of the specimens collected by Duellman (KU 163589, 3 km SW Uchumayo, at $2,150 \mathrm{~m}$ asl). During the following years, the regional museums of Peru considered the population from "La Caldera batholith" as an undescribed form associated with Liolaemus insolitus (Zeballos et al. 2002), which they called Liolaemus cf. insolitus. Nuñez (2004) identified the specimen considered by Boulenger (1885) as a new species of the genus Phrynosaura (synonym of Liolaemus). Gutiérrez and Quiroz (2010), based on photographic material, presumed that the population belonged to L. cf. insolitus. Later, Langstroth (2011) reviewed the field notes written by Duellman, Simmons, and Pefaur (unpublished) and their specimens cataloged as Phrynosaura stolzmanni from the University of Kansas (KU 163589, KU 163592, and KU 163594; collected from " 10 km SE of the town of Uchumayo, in the La Caldera batholith"), and indicated that these lizards are not Liolaemus stolzmanni. Based on fieldnotes, which indicate that these specimens are individuals found in habitats of gray sand with granitic rocks and the coloration is cryptic with the habitat, he also highlights the mottled black, orange, and metallic blue back, and the lateral sides of the belly are orange; and these characters are corroborated with the photography of the individual KU163589; citing this population in his work as Liolaemus species 2 (KU 163589, KU 163592, and KU 163594). Finally, Abdala et al. (2020) corroborate through

Huamaní-Valderrama et al.


Fig. 11. Phylogenetic trees showing the relationships between Liolaemus anqapuka sp. nov. and species within the L. montanus group by (A) Total Evidence analysis, (B) molecular phylogenetic analysis, and (C) morphological phylogenetic analysis. The values correspond to the support measure with symmetric resampling.
analysis of Total Evidence of the L. montanus group that the population from "La Caldera batholith" ( $L$. aff. insolitus7) is an independent terminal, because it presents morphological characteristics different from the rest of the known species of Liolaemus. Therefore, we corroborate the hypothesis presented by Abdala et al. (2020), based in morphological and molecular phylogenetic evidence, which they named as $L$. aff. insolitus 7 .

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 of Peru. Roberto is currently the Curator and Principal Researcher of the Herpetological Collection, Museum of Natural History, National University of San Augustin de Arequipa, Peru, and Vice President and Founding Member of the Herpetological Association of Peru (AHP). He is interested in the herpetofauna of the tropical Andes and the coastal desert, with a special focus on lizards of genus Liolaemus, and is developing studies in the systematics of amphibians and reptiles, ecology, and conservation. Roberto has conducted several biodiversity inventories, biological assessments, and biodiversity monitoring programs, and is currently working at the Natural Protected Areas Service of the Peruvian Ministry of Environment.


Álvaro Aguilar-Kirigin is a Bolivian Biologist who graduated from the Universidad Mayor de San Andrés, La Paz, has been a researcher at the Colección Boliviana de Fauna specializing in herpetology since 2002, and is a member of the Bolivian Network Researchers in Herpetology. He carried out two research internships in Argentina and Uruguay, focusing on the systematics and phylogeny of Liolaemus and the latitudinal patterns of seasonal changes in fat body size in 59 species of lizards. He has authored over 35 publications ( 18 of which were peer-reviewed), 10 book chapters, and seven technical cards as part of book chapters, including the descriptions of three species of Liolaemus. Álvaro is interested in integrative taxonomy, especially in the genus Liolaemus, because of its phenotypic plasticity in the Andean region. As a line of research, he is making progress with linear models in the study of classical comparative morphometry. Likewise, he is linked to the conservation of the wildlife that inhabit the Amazonian forest in the Department of Beni in Bolivia.


Wilson Huanca-Mamani is a Biologist from the Universidad de Concepción (Concepción, Chile), with a Doctorate in Plant Biotechnology from Centro de Investigación y de Estudios Avanzados del IPN (CINVESTAV), Unidad Irapuato, Mexico. Wilson is currently a researcher at the Universidad de Tarapacá (Arica, Chile). One of his research interests focuses on the population genetics of desert plants.


Pablo Valladares-Faúndez is a Biologist who graduated from the Austral University of Chile and obtained his Ph.D. from the University of Chile. Pablo is currently an academic in the Department of Biology, Science Faculty, University of Tarapaca, in northern Chile. He is interested in the study of vertebrates from arid and high Andean ecosystems, particularly lizards of the genera Liolaemus and Microlophus, and is developing studies on their taxonomy, systematics, ecology, and conservation. Pablo is also developing a herpetological collection of northern Chile.

José Cerdeña is a Biologist who graduated from the Universidad Nacional de San Agustín de Arequipa (Peru), and is a researcher at Museo de Historia Natural de la Universidad Nacional de San Agustín de Arequipa (MUSA) in Peru. José's research includes the systematics, taxonomy, and biogeography of Lepidoptera, but with a recent interest in the taxonomy and ecology of the genus Liolaemus in southern Peru.

Juan C. Chaparro is a Peruvian Biologist with extensive experience in studying the fauna of all the traditional
 geographic regions of Peru. Juan graduated in Biological Sciences from Universidad Nacional Pedro Ruiz Gallo, Lambayeque, Peru; received a Master's degree in Biodiversity in Tropical Areas and Conservation in 2013, from an institutional consortium of the International University of Menendez Pelayo (UIMP-Spain), Universidad Tecnológica Indoamérica (UTI-Ecuador), and Consejo Superior de Investigaciones Científicas (CSIC-Spain). He is currently the president of the Herpetological Association of Peru (AHP), director and curator of the Herpetological Collection of the Museo de Biodiversidad del Perú (MUBI, https://mubi-peru.org/herpetologia/p-mubi), and he also works as a consultant in environmental studies. Juan has authored or co-authored 51 peer-reviewed scientific papers, notes, book chapters, and books on various fauna (especially in herpetology and arachnology), on topics such as their taxonomy, biodiversity, systematics, phylogeny, conservation, and biogeography in South America. He is interested in those topics, as well as life history, distributional patterns, and evolution using amphibian and reptiles as biological models. Four species have been named in his honor: Phyllomedusa chaparroi (Amphibia), Phrynopus chaparroi (Amphibia), Hadruroides juanchaparroi (Arachnida), and Chlorota chaparroi (Insecta).


Roy Santa Cruz is a Research Associate at Área de Herpetología del Museo de Historia Natural (MUSA), Universidad Nacional de San Agustín de Arequipa, Peru. His current research interests include the taxonomy, natural history, and conservation of amphibians and reptiles. He currently coordinates several research projects which focus on threatened species of Andean frogs.

Cristian S. Abdala is an Argentinian Biologist, a researcher at CONICET, and a professor at the Universidad Nacional de Tucumán (UNT) in Argentina. Cristian received his Ph.D. degree from UNT, and is a herpetologist with extensive experience in the taxonomy, phylogeny, and conservation of Liolaemus lizards. He has authored or co-authored over 70 peer-reviewed papers and books on herpetology, including the descriptions of 50 recognized lizard species, mainly in genus Liolaemus. One species, Liolemus abdalai, has been named in his honor. He has conducted several expeditions through Patagonia, the high Andes, Puna, and the salt flats of Argentina, Chile, Bolivia, and Peru. Since 2016, Christian has been the president of the Argentine Herpetological Association.

## Appendix I. Specimens examined.

Liolaemus anqapuka sp. nov. ( $n=22$ ): PERU. Arequipa: Arequipa, Uchumayo: MUBI 13521-22, MUSA 4131, 4133-34; Arequipa, Uchumayo, Quebrada Tinajones, MUSA 1766-67, MUSA 4546, 5207-12, 5214, MUBI 14417, MUBI 14680, LSF 001, LSF 002; Arequipa, Uchumayo, between Quebrada Tinajones and Quebrada San Jose, MUSA 5573-75.

Liolaemus balagueri $(n=18)$ : PERU. Arequipa: Camaná, Quilca, Lomas de Quilca, MUSA 1772-74, MUSA 5575-78, MUBI 13206-09, MUBI 16483-84, MUSM 39193-95; Camaná, Camaná, Lomas de La Chira, MUSM 39192, MUSA 5579.

Liolaemus chiribaya ( $n=11$ ): PERU. Moquegua: Mariscal Nieto, Torata, Jaguay Chico, MUSM 31548-50, MUSM 31553; Mariscal Nieto, Torata, Cerro los Calatos, MUSM 31547, MUSM 31386, MUSM 31388-91; Mariscal Nieto, between Moquegua and Torata, MUSM 31387.

Liolaemus etheridgei $(n=17)$ : PERU. Arequipa: Cabrerías, Cayma, MUSA 501; Cerro Uyupampa, Sabandia, MUSA 54954; Monte Ribereño de la Quebrada de Tilumpaya Chiguata. Pocsi, MUSA 1113-14, 1116, 1264-68, 1353; Anexo de Yura Viejo, Yura, MUSA 1229.

Liolaemus evaristoi $(n=16)$ : PERU. Huancavelica: Los Libertadores, Pilpichaca, Huaytara, MUSA 2841 (holotype), 278185, 2840, 2842-45, MUBI 10474-78 (paratypes).

Liolaemus insolitus $(n=10)$ : PERU. Arequipa: Lomas de Mejía, Deán Valdivia, MUSA 346, MUSA 1741, MUSA 2187-90; Alto Inclan, Mollendo MUSA 4787-88, MUSA 4812, MUSA 4815.

Liolaemus nazca $(n=7)$ : PERU. Ica: Nazca, MUSM 31520-21, MUSM 31523, MUSM 31525-26, MUSM 31541, MUSM 16100.

Liolaemus poconchilensis ( $n=2$ ): PERU. Tacna: Morro Sama, Las Yaras, MUSA 1638-39.
Liolaemus polystictus ( $n=13$ ): PERU. Huancavelica: Mountain near Rumichaca, Pilpichaca, MUSA 1337-1338; Santa Inés, Castrovirreyna, MUSA 2448-2457; Santa Inés, FML 1683 (paratype).

Liolaemus robustus ( $n=11$ ): PERU. Lima: Surroundings of Huancaya, Reserva Paisajistica Nor Yauyos Cochas, MUSA 1693-1702; Junín: Junín, FML 1682 (paratype).

Liolaemus signifer ( $n=12$ ): PERU. Puno: Titicaca Lake, $3,840 \mathrm{~m}$, FML 1434; Titicaca Lake, road to Puno, FML 1557; near Tirapata, MUSA 1415; Huancané, Comunidad Taurahuta, MUSA 1441-43; Huerta Huayara community, 3 km before Puno, MUSA 1483-87.

Appendix II. Measured morphometric traits and meristic characters.

| Morphological <br> characters | L. balagueri <br> $\boldsymbol{n}=\mathbf{1 2}$ | L. chiribaya <br> $\boldsymbol{n}=\mathbf{1 0}$ | L. insolitus <br> $\boldsymbol{n}=\mathbf{1 5}$ | L. $\boldsymbol{n a z c a}$ <br> $\boldsymbol{n}=\mathbf{7}$ | L. anqapuka sp. nov. <br> $\boldsymbol{n}=\mathbf{7}$ |
| :---: | :---: | :---: | :---: | :---: | :---: |
| SVL | $51.08-64.96$ | $49.28-68.25$ | $47.35-65.77$ | $53.51-64.34$ | $52.15-73.53$ |
|  | $58.82 \pm 4.68$ | $59.60 \pm 6.59$ | $56.79 \pm 5.41$ | $59.35 \pm 4.98$ | $60.14 \pm 6.71$ |
| DN | $1.03-2.04$ | $1.96-3.00$ | $0.91-1.96$ | $0.63-1.81$ | $0.96-1.68$ |
|  | $1.31 \pm 0.28$ | $2.47 \pm 0.30$ | $1.53 \pm 0.36$ | $1.47 \pm 0.42$ | $1.36 \pm 0.24$ |
| AH | $3.59-5.61$ | $3.71-5.67$ | $3.21-5.06$ | $1.96-4.85$ | $4.16-5.43$ |
|  | $4.45 \pm 0.54$ | $4.73 \pm 0.66$ | $4.23 \pm 0.53$ | $3.92 \pm 0.93$ | $4.70 \pm 0.42$ |
| NC | $1.65-2.91$ | $1.07-2.57$ | $1.52-2.85$ | $2.10-3.14$ | $2.10-2.73$ |
|  | $2.09 \pm 0.36$ | $2.09 \pm 0.52$ | $2.09 \pm 0.33$ | $2.49 \pm 0.38$ | $2.47 \pm 0.27$ |
| EO | $6.11-8.96$ | $7.01-9.26$ | $7.12-8.88$ | $6.16-8.25$ | $7.00-9.62$ |
|  | $7.49 \pm 0.74$ | $8.24 \pm 0.72$ | $7.90 \pm 0.49$ | $7.11 \pm 0.80$ | $8.54 \pm 0.90$ |
| LEI | $0.89-1.69$ | $0.88-1.28$ | $0.66-1.58$ | $0.47-2.06$ | $1.23-1.76$ |
|  | $1.28 \pm 0.26$ | $1.09 \pm 0.14$ | $1.12 \pm 0.26$ | $1.31 \pm 0.48$ | $1.54 \pm 0.21$ |
| PA | $0.85-1.74$ | $1.31-1.72$ | $0.90-1.82$ | $0.51-1.91$ | $1.45-1.99$ |
|  | $1.34 \pm 0.26$ | $1.43 \pm 0.14$ | $1.25 \pm 0.26$ | $1.24 \pm 0.47$ | $1.77 \pm 0.21$ |
| AM | $1.05-1.76$ | $2.00-2.86$ | $1.32-2.41$ | $0.46-1.31$ | $1.06-1.49$ |
|  | $1.28 \pm 0.20$ | $2.46 \pm 0.28$ | $1.94 \pm 0.47$ | $1.06 \pm 0.30$ | $1.26 \pm 0.18$ |

Appendix II (continued). Measured morphometric traits and meristic characters.

| Morphological characters | L. balagueri $n=12$ | L. chiribaya $n=10$ | L. insolitus $n=15$ | L. nazca $n=7$ | L. anqapuka sp. nov. $n=7$ |
| :---: | :---: | :---: | :---: | :---: | :---: |
| LM | 2.05-3.13 | 0.84-1.55 | 1.08-2.92 | 1.23-2.64 | 2.30-2.78 |
|  | $2.53 \pm 0.34$ | $1.20 \pm 0.22$ | $1.69 \pm 0.66$ | $2.16 \pm 0.54$ | $2.55 \pm 0.21$ |
| NB | 1.11-1.92 | 1.19-1.63 | 0.96-1.56 | 1.16-1.87 | 0.97-1.51 |
|  | $1.41 \pm 0.23$ | $1.42 \pm 0.12$ | $1.26 \pm 0.18$ | $1.56 \pm 0.28$ | $1.31 \pm 0.17$ |
| HR | 0.40-1.04 | 0.64-1.22 | 0.53-1.01 | 0.69-1.54 | 0.55-1.04 |
|  | $0.80 \pm 0.17$ | $0.86 \pm 0.19$ | $0.77 \pm 0.11$ | $0.93 \pm 0.31$ | $0.82 \pm 0.15$ |
| ES | $2.83-4.58$ | 3.20-4.06 | 1.90-4.16 | 2.93-6.62 | 3.24-4.73 |
|  | $3.72 \pm 0.49$ | $3.57 \pm 0.27$ | $3.52 \pm 0.53$ | $3.93 \pm 1.26$ | $3.81 \pm 0.49$ |
| hTy | 1.69-2.63 | 1.68-2.30 | 1.02-2.09 | 1.72-2.49 | 1.37-2.02 |
|  | $2.16 \pm 0.26$ | $1.91 \pm 0.21$ | $1.72 \pm 0.25$ | $1.95 \pm 0.26$ | $1.78 \pm 0.23$ |
| aTy | 0.47-1.54 | 1.18-1.65 | 0.65-1.22 | 0.67-1.13 | 0.57-1.10 |
|  | $0.97 \pm 0.26$ | $1.37 \pm 0.17$ | $0.94 \pm 0.20$ | $0.94 \pm 0.14$ | $0.85 \pm 0.18$ |
| LPO | 0.91-1.67 | 0.57-1.54 | 0.53-1.49 | 0.75-2.35 | 0.60-1.07 |
|  | $1.20 \pm 0.23$ | $1.02 \pm 0.32$ | $1.17 \pm 0.24$ | $1.43 \pm 0.50$ | $0.89 \pm 0.19$ |
| LPOT | 0.43-0.85 | 0.48-0.80 | 0.37-0.72 | 0.48-0.92 | 0.33-0.82 |
|  | $0.61 \pm 0.13$ | $0.60 \pm 0.11$ | $0.52 \pm 0.11$ | $0.69 \pm 0.15$ | $0.55 \pm 0.18$ |
| LCSP | 1.01-2.00 | 0.83-1.42 | 0.54-1.52 | 1.39-3.36 | 0.66-1.37 |
|  | $1.52 \pm 0.34$ | $1.14 \pm 0.19$ | $1.03 \pm 0.25$ | $2.01 \pm 0.67$ | $1.03 \pm 0.31$ |
| LCLB | 0.68-1.56 | 0.86-1.28 | $0.55-131$ | 0.85-2.14 | 0.57-1.30 |
|  | $1.15 \pm 0.25$ | $0.99 \pm 0.12$ | $0.97 \pm 0.20$ | $1.29 \pm 0.46$ | $1.03 \pm 0.28$ |
| DEO | $6.80-8.83$ | 7.31-9.32 | 7.48-9.17 | 6.90-8.67 | 8.17-10.95 |
|  | $7.83 \pm 0.67$ | $8.26 \pm 0.68$ | $8.36 \pm 0.55$ | $7.58 \pm 0.71$ | $9.45 \pm 1.03$ |
| 1D | 1.86-3.21 | 1.84-3.12 | 1.63-2.95 | 1.61-2.82 | 2.56-3.31 |
|  | $2.51 \pm 0.39$ | $2.52 \pm 0.44$ | $2.32 \pm 0.31$ | $2.13 \pm 0.41$ | $2.88 \pm 0.30$ |
| G4D | 1.10-1.59 | 0.74-1.38 | 1.17-2.04 | 0.67-1.35 | 1.29-2.11 |
|  | $1.30 \pm 0.16$ | $1.01 \pm 0.21$ | $1.53 \pm 0.22$ | $1.00 \pm 0.23$ | $1.54 \pm 0.32$ |
| 5D | $2.89-3.84$ | 2.41-4.41 | 2.44-3.40 | 2.33-3.93 | 2.28-3.41 |
|  | $3.29 \pm 0.33$ | $3.31 \pm 0.56$ | $2.84 \pm 0.25$ | $2.93 \pm 0.52$ | $3.00 \pm 0.44$ |
| AHU | 1.98-3.63 | 1.99-4.58 | 2.24-3.46 | 2.01-3.93 | 2.59-4.36 |
|  | $2.81 \pm 0.51$ | $3.03 \pm 0.78$ | $2.77 \pm 0.38$ | $3.06 \pm 0.54$ | $3.45 \pm 0.60$ |
| LEA1 | $6.94-11.83$ | $8.65-10.81$ | 6.34-9.45 | 7.01-8.95 | $9.03-11.01$ |
|  | $8.89 \pm 1.40$ | $9.75 \pm 0.71$ | $8.19 \pm 0.86$ | $8.17 \pm 0.80$ | $9.96 \pm 0.68$ |
| AMU | $3.76-5.28$ | 3.33-4.98 | $2.67-4.68$ | 4.82-7.19 | $3.60-5.80$ |
|  | $4.54 \pm 0.47$ | $4.18 \pm 0.60$ | $3.71 \pm 0.73$ | $5.96 \pm 0.79$ | $4.43 \pm 0.78$ |
| 1P | 2.87-3.68 | 1.66-4.30 | 2.50-3.78 | 1.73-4.08 | 2.51-3.42 |
|  | $3.19 \pm 0.29$ | $3.20 \pm 0.86$ | $3.15 \pm 0.37$ | $2.92 \pm 0.72$ | $3.08 \pm 0.29$ |
| 4 U | 0.93-2.06 | 0.74-2.32 | 0.98-1.77 | 0.75-1.72 | 0.97-1.87 |
|  | $1.45 \pm 0.32$ | $1.33 \pm 0.45$ | $1.30 \pm 0.22$ | $1.33 \pm 0.36$ | $1.45 \pm 0.32$ |
| AL | 16.19-20.03 | 19.64-33.02 | 12.12-19.74 | 19.61-27.88 | 15.27-24.37 |
|  | $17.43 \pm 1.06$ | $25.76 \pm 4.97$ | $15.99 \pm 2.40$ | $24.85 \pm 2.70$ | $19.85 \pm 3.27$ |
| WTB | 6.32-8.63 | 6.19-9.15 | 4.91-8.44 | 6.24-9.20 | 6.50-10.07 |
|  | $7.49 \pm 0.76$ | $7.76 \pm 1.21$ | $6.98 \pm 1.07$ | $7.46 \pm 0.88$ | $7.46 \pm 1.20$ |
| ASPI | 5.39-6.80 | $4.37-7.80$ | 5.57-7.84 | $2.70-7.20$ | 4.76-6.66 |
|  | $6.08 \pm 0.44$ | $6.45 \pm 1.17$ | $6.43 \pm 0.69$ | $4.55 \pm 1.35$ | $5.56 \pm 0.64$ |

Appendix II (continued). Measured morphometric traits and meristic characters.

| Morphological characters | L. balagueri $n=12$ | L. chiribaya $n=10$ | L. insolitus $n=15$ | L. nazca $n=7$ | L. anqapuka sp. nov. $n=7$ |
| :---: | :---: | :---: | :---: | :---: | :---: |
| LPI | 4.01-6.12 | 4.71-6.75 | 3.73-6.40 | 3.23-6.16 | 5.20-9.22 |
|  | $5.07 \pm 0.62$ | $5.75 \pm 0.76$ | $5.03 \pm 0.82$ | $4.90 \pm 0.87$ | $6.33 \pm 1.41$ |
| Al1 | 4-8 | 5-7 | 5-9 | 5-8 | 6-8 |
|  | $6.33 \pm 0.98$ | $6.20 \pm 0.63$ | $6.27 \pm 1.16$ | $6.14 \pm 1.07$ | $7.00 \pm 0.58$ |
| A12 | 6-8 | 7-9 | 7-8 | 6-9 | 7-10 |
|  | $7.08 \pm 0.79$ | $7.60 \pm 0.70$ | $7.47 \pm 0.52$ | $7.43 \pm 0.98$ | $8.43 \pm 0.98$ |
| A15 | 6-8 | 7-10 | 7-9 | 6-8 | $8-10$ |
|  | $6.67 \pm 0.89$ | $8.60 \pm 0.97$ | $7.80 \pm 0.56$ | $6.57 \pm 0.98$ | $9.00 \pm 0.82$ |
| A13 | 5-7 | 5-7 | 5-8 | 5-6 | 6-8 |
|  | $6.08 \pm 0.51$ | $6.10 \pm 0.57$ | $6.40 \pm 0.74$ | $5.57 \pm 0.53$ | $6.86 \pm 0.69$ |
| A19 | 5-7 | 5-7 | 5-8 | 5-6 | 7-8 |
|  | $5.67 \pm 0.65$ | $6.10 \pm 0.57$ | $6.27 \pm 0.70$ | $5.71 \pm 0.49$ | $7.14 \pm 0.38$ |
| A14 | 4 | 4-6 | 4-6 | 4-5 | 4-5 |
|  | $4.00 \pm 0.00$ | $4.20 \pm 0.63$ | $4.67 \pm 0.82$ | $4.14 \pm 0.38$ | $4.14 \pm 0.38$ |
| A16 | 6-8 | 6-7 | 6-8 | 5-6 | 6-7 |
|  | $6.67 \pm 0.65$ | $6.10 \pm 0.32$ | $7.07 \pm 0.59$ | $5.86 \pm 0.38$ | $6.14 \pm 0.38$ |
| A17-1 | 7-9 | 5-8 | 7-8 | 7-10 | $8-10$ |
|  | $7.50 \pm 0.67$ | $6.40 \pm 1.07$ | $7.20 \pm 0.41$ | $8.43 \pm 0.98$ | $9.00 \pm 0.82$ |
| A18 | 12-16 | 14-18 | 14-18 | 11-14 | 13-17 |
|  | $13.75 \pm 1.29$ | $15.90 \pm 1.20$ | $15.07 \pm 1.03$ | $12.71 \pm 1.11$ | $14.29 \pm 1.50$ |
| A20-1 | 7-8 | 7-8 | 6-9 | 7-10 | 7-9 |
|  | $7.33 \pm 0.49$ | $7.30 \pm 0.48$ | $7.67 \pm 1.11$ | $8.71 \pm 1.11$ | $8.29 \pm 0.76$ |
| A20-2 | 9-11 | 11-13 | $8-16$ | 12-13 | 9-13 |
|  | $10.17 \pm 0.83$ | $12.60 \pm 0.84$ | $12.07 \pm 2.49$ | $12.86 \pm 0.38$ | $11.29 \pm 1.38$ |
| A20-3 | 14-16 | 14-16 | 12-16 | 15-19 | 11-15 |
|  | $14.67 \pm 0.65$ | $15.30 \pm 0.67$ | $14.40 \pm 1.30$ | $15.86 \pm 1.57$ | $13.57 \pm 1.62$ |
| A20-4 | 12-18 | 17-19 | 10-17 | 17-20 | 15-18 |
|  | $15.33 \pm 1.67$ | $18.20 \pm 0.92$ | $12.73 \pm 2.02$ | $18.57 \pm 1.13$ | $17.00 \pm 1.15$ |
| A20-5 | $8-11$ | 8 | 6-10 | 9-10 | 7-10 |
|  | $9.58 \pm 0.79$ | $8.00 \pm 0.00$ | $7.73 \pm 1.10$ | $9.71 \pm 0.49$ | $8.71 \pm 1.11$ |
| A21-1 | 5-10 | 9-10 | 6-11 | 8-10 | 7-11 |
|  | $8.17 \pm 1.53$ | $9.20 \pm 0.42$ | $7.80 \pm 1.15$ | $8.86 \pm 0.90$ | $9.29 \pm 1.50$ |
| A21-2 | 10-13 | 11-12 | 10-12 | 12-13 | 11-14 |
|  | $11.83 \pm 0.94$ | $11.20 \pm 0.42$ | $10.93 \pm 0.88$ | $12.71 \pm 0.49$ | $12.00 \pm 1.00$ |
| A21-3 | 9-18 | 14-16 | 12-16 | 15-18 | 12-18 |
|  | $15.00 \pm 2.37$ | $15.40 \pm 0.70$ | $14.00 \pm 1.25$ | $16.14 \pm 1.21$ | $15.14 \pm 1.86$ |
| A21-4 | 19-24 | 18-21 | 20-22 | 20-23 | 20-23 |
|  | $20.33 \pm 1.50$ | $19.50 \pm 0.85$ | $20.67 \pm 0.62$ | $21.57 \pm 0.98$ | $21.43 \pm 1.13$ |
| A21-5 | 10-14 | 11-13 | 10-12 | 10-13 | 9-13 |
|  | $11.58 \pm 1.16$ | $12.50 \pm 0.71$ | $11.27 \pm 0.88$ | $11.57 \pm 1.51$ | $10.86 \pm 1.35$ |
| A22 | 52-56 | 52-63 | 58-69 | 53-56 | 60-76 |
|  | $53.50 \pm 1.62$ | $57.40 \pm 3.50$ | $63.40 \pm 3.48$ | $54.14 \pm 1.35$ | $67.29 \pm 5.59$ |
| A26 | 0-7 | 2-5 | 0-8 | 1-6 | 2-6 |
|  | $3.00 \pm 2.80$ | $3.80 \pm 1.03$ | $4.20 \pm 2.83$ | $3.43 \pm 1.51$ | $3.43 \pm 1.62$ |

Appendix II (continued). Measured morphometric traits and meristic characters.

| Morphological characters | L. balagueri $n=12$ | L. chiribaya $n=10$ | L. insolitus $n=15$ | L. nazca $n=7$ | L. anqapuka sp. nov. $n=7$ |
| :---: | :---: | :---: | :---: | :---: | :---: |
| M2 | 1-2 | 2 | 1 | 1-3 | 1-2 |
|  | $1.33 \pm 0.49$ | $2.00 \pm 0.00$ | $1.00 \pm 0.00$ | $1.86 \pm 0.69$ | $1.86 \pm 0.38$ |
| M3 | 6-9 | 7-8 | 5-9 | 6-9 | 7-8 |
|  | $7.50 \pm 0.80$ | $7.20 \pm 0.42$ | $7.07 \pm 1.28$ | $7.57 \pm 1.13$ | $7.43 \pm 0.53$ |
| M5 | 3-5 | 3-5 | 4-8 | 4-6 | 5-6 |
|  | $4.25 \pm 0.62$ | $4.00 \pm 0.47$ | $6.73 \pm 0.96$ | $4.71 \pm 0.76$ | $5.29 \pm 0.49$ |
| M4 | 3-6 | 3-5 | 3-8 | 3-6 | 4-7 |
|  | $4.75 \pm 0.87$ | $3.80 \pm 0.63$ | $6.47 \pm 1.30$ | $4.86 \pm 1.07$ | $5.71 \pm 0.95$ |
| M13 | 1-6 | 2-6 | 5-16 | 4-11 | 3-8 |
|  | $3.92 \pm 1.68$ | $4.20 \pm 1.40$ | $10.00 \pm 3.21$ | $6.57 \pm 2.64$ | $5.29 \pm 1.80$ |
| M14 | 2-6 | 3-7 | 2-8 | 3-11 | 1-6 |
|  | $3.75 \pm 1.29$ | $4.40 \pm 1.07$ | $4.27 \pm 1.71$ | $7.86 \pm 2.97$ | $3.86 \pm 1.95$ |
| M15 | 1-6 | 1-8 | 5-24 | 1-12 | 1-4 |
|  | $3.50 \pm 1.51$ | $4.60 \pm 2.67$ | $12.53 \pm 5.05$ | $5.86 \pm 3.72$ | $2.29 \pm 1.25$ |
| M23 | 26-30 | 19-25 | 26-32 | 21-25 | 28-36 |
|  | $27.17 \pm 1.34$ | $21.70 \pm 1.89$ | $28.80 \pm 2.48$ | $23.86 \pm 1.46$ | $30.86 \pm 3.02$ |
| M26 | 52-60 | 55-66 | 52-60 | 54-59 | 63-72 |
|  | $56.50 \pm 2.28$ | $61.80 \pm 3.68$ | $55.80 \pm 2.27$ | $56.86 \pm 1.95$ | $67.29 \pm 3.15$ |
| M32 | 65-79 | 67-77 | 69-80 | 65-74 | 73-87 |
|  | $73.17 \pm 3.69$ | $72.70 \pm 2.95$ | $73.53 \pm 3.36$ | $70.57 \pm 2.88$ | $82.43 \pm 4.72$ |
| M34 | 1 | 1 | 2-4 | 1-2 | 1 |
|  | $1.00 \pm 0.00$ | $1.00 \pm 0.00$ | $2.87 \pm 0.52$ | $1.86 \pm 0.38$ | $1.00 \pm 0.00$ |
| D6 | 6-8 | 6-8 | 6-8 | 7-10 | 7-9 |
|  | $6.92 \pm 0.67$ | $7.30 \pm 0.67$ | $6.47 \pm 0.74$ | $7.71 \pm 1.11$ | $8.14 \pm 0.69$ |

Note: Range in the first line; mean $\pm$ standard deviation (mm) for quantitative characters in the second line.
Legend: Snout-vent length (SVL); minimum distance between the nasal scales (DN); snout width at the edge of the canthal scale (AH); distance from the nose to the back edge of the canthal scale (NC); distance between the posterior edge of the superciliary series (EO); length of the interparietal (LEI); length of the parietal (PA); mental scale width (AM); length of the mental scale (LM); distance from nostril to mouth (NB); rostral height (HR); length of the subocular scale (ES); auditory meatus height (hTy); auditory meatus width (aTy); length of the preocular scale (LPO); preocular width (LPOT); length of the fourth supralabial scale (LCSP); length of the fourth lorilabial scale (LCLB); length between orbits (DEO); length of the first finger of the forelimb, without claw (1D); length of the claw of the fourth finger of the forelimb (G4D); length of the fifth finger of the forelimb without claw (5D); humerus width (AHU); distance from the insertion of the forelimb in the body toward the elbow (LEA1); thigh width (AMU); length of the first toe of the hind limb without claw (1P); length of the claw of the fourth toe of the hind limb (4U); length of the five dorsal scales in a row in the middle of the body (ED); cloacal opening width, measured distance between the corners of the cloaca (PP); body width (AL); width of the base of the tail (WTB); upper width of the pygal area (ASPI); length of the pygal area (LPI). Number of scales around the interparietal scale (A11); number of supralabials on the right side (A12); number of supralabials on the left side (A15); number of infralabials on the right side (A13); number of infralabials on the left side (A19); number of scales around the mental scale (A14); number of scales around the rostral scale (A16); number of lorilabials (A17-1); Hellmich index (A18); subdigital lamellae of the first finger of the forelimb (A20-1); subdigital lamellae of the second finger of the forelimb (A20-2); subdigital lamellae of the third finger of the forelimb (A20-3); subdigital lamellae of the fourth finger of the forelimb (A20-4); subdigital lamellae of the fifth finger of the forelimb (A20-5); subdigital lamellae of the first toe of the hind limb (A21-1); subdigital lamellae of the second toe of the hind limb (A21-2); subdigital lamellae of the third toe of the hind limb (A21-3); subdigital lamellae of the fourth toe of the hind limb (A21-4); subdigital lamellae of the fifth toe of the hind limb (A21-5); number of dorsal scales between the occiput and the level of the anterior edge of the thigh (A22); number of precloacal pores (A26); number of scales between canthal and nasal scales (M2); number of scales around the nasal scale (M3); number of supraocular enlarged scales in the right side (M5); number of supraocular enlarged scales in the left side (M4); number of organs in the postrostral scales (M13); number of organs in the third lorilabial scale (M14); number of organs in the scale above the row of the lorilabial scales and below the canthal and preocular scales (M15); number of gular scales (M23); number of scales around midbody (M26); number of ventral scales (M32); number of auricular scales, projecting scales on anterior edge of auditory meatus (M34); and number of paravertebral spots in the right side (D6).

